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CONTENTS

Studies on the Nutritive Value of Spartina Grass Growing in the Marsh Areas of Coastal Georgia ..... *Paul B. Burkholder* 337

Some Grass Genera with Liquid Endosperm ..... *William C. Dore* 353

Epiphyllous Flowers. ..... *Harvey E. Stork* 363

Materials for a Dictionary of Botanical Terms—IV. Terms to Describe Apices. ..... *H. W. Bickett* 368

A Study of the Three-Dimensional Configurations of Sporogenous Cells in the Anthers of Trillium erectum L. with Special Reference to the Geometrical Aspects of Cell Shape. *Joan Elma Rahn* 377

Botanical Bibliographies: Classification, Form, Arrangement and Use. ..... *Josh McCormick* 377

Torreya

A Large Swamp White Oak of the Lower Raritan Flood Plain. By John W. Andresen. Field Trip Reports. Proceedings of the Club. Book Reviews. Notes. 382

Index to American Botanical Literature 391

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BULLETIN OF THE TORREY BOTANICAL CLUB
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STUDIES ON THE NUTRITIVE VALUE OF SPARTINA GRASS GROWING IN THE MARSH AREAS OF COASTAL GEORGIA[1]

PAUL R. BURKHOLDER[2]

Extensive low areas along the coast of Georgia are covered with marsh grasses. Among these, *Spartina alterniflora,* Loisel. contributes on a large scale to primary productivity in the marshes and shallow estuaries of the region. Especially luxuriant growth of this dark green grass, oftentimes attaining a height of six feet, occurs in the low marshes, along river banks and on the shores of islands. The grass of high marshland is yellow green in color, tougher, and generally less than two feet in height. The *Spartina* main crop grows during a long season from March to October. In protected places with southern exposure, however, the grass may show growth of tender green shoots even during the winter months. The crop apparently disintegrates slowly during the year or two following its maturation in the fall. Microbial conversion of grass and its consumption by small herbivores leads into the complex cycle of nutrition which supports crustaceans, fish, and fowl, all of which abound in the region.

During spring and early summer, cattle are known to graze on the salt marshes where *Spartina* is accessible. The grass is harvested in small quantities, for cattle feeding, by residents of the sea islands. The writer was told by Mr. Frank Durand, who resides on Sapelo Island, that in former years marsh grass was harvested as the sole feed for mules that were used to haul fuel for the wood-burning steam locomotives on the old Brunswick and Florida Railroad (Black 1952).

General observations of the extensive productivity and potential uses of *Spartina* in the coastal regions of Georgia prompted us to collect samples of the marsh grass for analysis of its nutritive content, with particular reference to its B vitamins and amino acids, known to be essential for growing animals.

Materials and methods. Four different samples of mature marsh grass were gathered from different locations, along river banks and on high marsh in the vicinity of Sapelo Island in the period August 14 to 27, 1955, and dried rapidly with heat supplied by 200-watt incandescent lamps. Young grass was harvested from a southern exposure on the bank of

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Georgia, NR163 308. Some of the work was done at the Marine Biology Laboratory, Sapelo Island, Georgia, and this paper is contribution No. 3 from that laboratory.

[2] The author's present address is Brooklyn Botanic Garden, Brooklyn 25, N.Y.

[THE BULLETIN for July–August, 1956 (83: 253–325) was issued August 20, 1956]

Lazaretta Creek, near Savannah, Georgia, on November 29, 1955, and dried with heat from a steam radiator. Dead grass stems from the preceding year's growth were gathered on August 27, 1955 from a pile left by a spring tide. These old stems were devoid of leaves, which long ago had disintegrated and washed away. The stems were dried over a steam radiator. A summary of the data concerning source materials is presented in Table 1.

TABLE 1. *Description of grass samples collected for chemical and microbiological analyses.*

Sample No.	Description	Source	Date Collected	Method of Drying	Air Dried Moisture Content Per Cent
1	Mature Terminal Leaf-stalks, 2 ft. long	Low Marsh, Jack Creek	August 14, 1955	Tungsten lamps	15.1
2	Mature Terminal Leaf-stalks, 1 ft. long	High Marsh, Barn Creek	August 20, 1955	Tungsten lamps	14.2
3	Mature Terminal Leaf-stalks, 2 ft. long	Low Marsh, Mud Creek	August 22, 1955	Tungsten lamps	15.7
4	Mature Whole plants, leaves and stems, 4–5 ft. long	Low Marsh, Jack Creek	August 27, 1955	Tungsten lamps	15.0
6	Young Terminal shoots. About 1½ ft. long	Low Marsh, Lazaretta Creek	November 29, 1955	Steam radiator	13.1
7	Weathered stems	Low Marsh, Duplin River	August 27, 1955	Steam radiator	8.7

The dried grass samples were prepared for analyses by grinding in a Wiley mill. All samples were kept in cardboard cartons until they could be analyzed. The moisture content was determined, prior to making the analyses, so that appropriate corrections could be made on an oven dry basis. Moisture content of the samples, determined at the time when proximate analyses were made, is shown in Table 1. The per cent of moisture at the time when vitamins and amino acids were determined was found to be as follows: sample no. one, 6.13; sample no. three, 6.38; and sample no. six, 8.77.

Determinations of moisture, fat, protein, crude fibre, ash, nitrogen-free extract, calcium, phosphorus, and iron were made according to the methods recommended in the 8th edition of the Official Methods of Analysis of the Association of Official Agricultural Chemists (1955). These analyses were made, on six different samples, by Law and Company, Atlanta, Georgia. The data have been calculated on a dry basis for the reports in Table 2 and Table 3.

Three samples of grass were analyzed for their content of ten B vitamins and ten essential amino acids by Food Research Laboratories, Long Island City, New York. The techniques recommended in Methods of Analysis of the Association of Official Agricultural Chemists (1955) were employed for the determination of thiamine, riboflavin, niacin, total folic acid, and vitamin B_{12} activity. Total pantothenic acid was assayed according to the procedure of Toepfer, Zook and Richardson (1954). Biotin and choline were determined according to the method outlined by Barton-Wright (1952). Pyridoxine was assayed by the technique of Parrish, Loy and Kline (1955). For the assay of inositol, the sample was hydrolyzed by the method of Jurist and Foy (1944), and the determination was made according to the general procedure of Atkin, Schultz, Williams, and Frey

TABLE 2. *Proximate analyses of different samples of marsh grass and Coastal Bermuda Grass.*[3] *Values are given as per cent of dry weight, and energy as therms per lb.*

Analyses	Samples 1 Mature Leaves	2 Mature Leaves	3 Mature Leaves	4 Mature Leaves and Stems	6 Young Leaves	7 Weathered Stems	Coastal Bermuda Grass
Fat	2.80	2.39	2.39	2.15	2.98	0.78	2.0
Protein	8.51	5.68	9.78	7.86	13.24	4.04	13.1
Crude Fibre	29.38	27.87	31.01	31.20	29.75	35.63	33.0
Ash	9.84	11.72	11.48	10.63	12.83	13.85	4.6
Nitrogen-free Extract	49.47	52.34	45.34	48.16	40.20	45.70	47.3
Therms	1.70	1.63	1.64	1.69	1.68	1.68	—

[3] Data for Coastal Bermuda Grass (Burton 1948) are shown in the last column for comparison.

(1943). With the exception of the thiochrome method for determination of thiamine, all of the methods for assay of the B vitamins were microbiological. The resulting data are reported in Table 4 as milligrams per 100 grams of dry weight.

The ten amino acids were determined on properly hydrolyzed samples by means of microbiological procedures summarized in the book by Barton-Wright (1952). The data, presented in Table 5, show the per cent of each amino acid on a dry weight basis, and also the per cent of each compound calculated on the basis of nitrogen taken to be 16. This latter expression gives an approximate per cent of individual amino acids in the mixed proteins of the dried grass.

Discussion of data. Proximate analyses, given in Table 2, show minor variations among the different samples of grass. Most interesting is the

high per cent of protein, 13.24, in rapidly growing young leafy shoots of sample no. 6. The weathered stems, devoid of leaves after a year, show loss of fat and protein resulting from processes of disintegration. Crude fibre seems to persist in the weathered stems, that float and sometimes remain on the beaches for a long while. Comparison of the data for *Spartina* and proximate analyses made on Coastal Bermuda Grass (Burton 1948), shown in the last column of Table 2, indicate a similarity in composition. All of the *Spartina* samples, however, show a higher content of ash, probably because of their sea water habitat. Determinations of therms per pound by colorimetry yield data similar to the values obtained by calculation, on the basis of 4 calories per gm. of protein or carbohydrate, and 9 calories per gm. of fat.

TABLE 3. *Some mineral values of Spartina expressed as per cent of each element in the dried grass.*

Minerals	Samples					
	1	2	3	4	6	7
	Mature Leaves	Mature Leaves	Mature Leaves	Mature Leaves and Stems	Young Leaves	Weathered Stems
Ca	1.03	0.71	1.47	0.39	0.90	0.64
P	0.17	0.13	0.18	0.14	0.25	0.05
Fe	0.06	0.18	0.15	0.12	0.29	0.27

The mineral values, shown in Table 3, indicate some variations among the samples of *Spartina*. Of particular interest is the loss of calcium and phosphorus from the weathered stems, and the apparent retention of iron in these stems.

The data in Table 4 indicate that growth factors of the B vitamin complex are present in marsh grass, probably in adequate amounts to

TABLE 4. *Vitamin content of marsh grasses expressed as mg. per 100 gm. dry weight. Source of samples is given in Table 2.*

Vitamins	Samples		
	2	3	6
	Mature Leaves	Mature Leaves	Young Leaves
Thiamine	0.026	0.056	0.037
Riboflavin	0.640	0.725	1.360
Niacin	1.750	2.140	3.520
Pantothenic acid (Total)	1.850	0.768	1.870
Biotin	0.012	0.010	0.018
Folic acid (Total)	0.288	0.459	0.483
Vitamin B_{12} Activity	0.001	0.001	0.002
Pyridoxine	0.418	1.210	0.915
Choline	47.600	61.000	76.500
Inositol	25.600	25.600	43.900

supply requirements of certain exacting microorganisms that may live in the marsh environment. From the amount of growth factor required for half-maximum growth by the microorganisms employed in making assays of these B vitamins (Barton-Wright 1952), it is possible to calculate the corresponding dilutions of the dried grass in aqueous media, that would yield equivalent concentrations for half-maximum growth. These calculated dilution factors are given in Table 6. Each value represents the factor which, when multiplied by 100 gm. of grass, would give the grams of medium that would contain sufficient vitamin to permit half-maximum growth of heterotrophic microorganisms. It is obvious that vitamin-requiring bacteria should find more than adequate levels of these compounds, while growing on or near decomposing grass in the marsh regions.

TABLE 5. *Amino acid content of marsh grass expressed in per cent (gm. amino acid per 100 gm. of dry material), and as per cent on the basis of N[4] = 16. The source of samples is given in Table 2.*

Amino Acids	Samples					
	2		3		6	
	Mature Leaves		Mature Leaves		Young Leaves	
	Dry Basis	N = 16	Dry Basis	N = 16	Dry Basis	N = 16
Arginine	0.214	1.97	0.182	1.61	0.230	1.42
Leucine	0.362	3.33	0.214	1.89	0.307	1.89
Isoleucine	0.224	2.07	0.143	1.26	0.252	1.57
Lysine	0.436	4.03	0.769	6.77	0.866	5.35
Methionine	0.026	0.240	0.038	0.337	0.094	0.579
Phenylaline	0.149	1.37	0.128	1.135	0.187	1.15
Tryptophan	0.058	0.534	0.086	0.76	0.124	0.765
Histidine	0.010	0.092	0.028	0.248	0.039	0.241
Valine	0.088	0.710	0.149	1.31	0.197	1.21
Threonine	0.138	1.27	0.256	2.26	0.829	2.03

[4] The per cent of nitrogen on a dry basis was as follows: No. 2, 1.74; No. 3, 1.81; No. 6, 2.59.

The presence of trace amounts of vitamin B_{12} activity in the grass, as determined in the *Lactobacillus leichmannii* assay, has been observed also in separate assays performed with the *E. coli* mutant technique (Burkholder and Burkholder 1956). It appears possible that cobalamine formed by microorganisms growing in the water and mud of the region may have contributed to the assays, either as adhering matter or by absorption of the vitamin into the tissues of the plants.

Further inspection of the data in Table 4 suggests that adequate levels of B vitamins are present in dried grass to satisfy growth of the guinea pig, with the exception of thiamine and folic acid (Jukes and Stoksdad 1951, Mannering 1949). It is, of course, difficult to assess the vitamin requirements of marine animals with our present state of knowledge.

The data in Table 5 indicate that the proportion of amino acids in the

proteins of *Spartina alterniflora*, Loisel. is unusual in several respects. If one compares the amino acid composition of the leaves of representative species in the family of grasses (Lugg 1949) with *Spartina*, it becomes apparent that the latter has a relatively low per cent content of such compounds as arginine, leucine, isoleucine, methionine, and histidine. The most striking deviation is found in the case of arginine. According to the data compiled by Lugg (1949), leaves of the Gramineae contain about 13.7 per cent of arginine in their protein, whereas, in Table 5 only 1.61 per cent of arginine is reported for the protein of *Spartina*. Further consideration of the protein composition of marine fish and shellfish (Walford and Wilber 1955) indicates that for these marine animals, *Spartina* proteins would have somewhat limited biological value because of their relatively low content of arginine, the leucines, methionine, phenylalanine, histidine,

TABLE 6. *Calculated dilution factors*[5] *of dried grass (Sample No. 3) which when placed in aqueous media would produce extracts containing an equivalent amount of each factor for half maximum growth of typical assay microorganisms.*

Vitamins	Dilution Factor
Thiamine	200
Riboflavin	1,200
Niacin	1,400
Pantothenic acid	3,800
Biotin	10,000
Folic acid	10
Vitamin B_{12}	170
Pyridoxine	240
Choline	800
Inositol	340

[5] Dilution Factor (D. F.) = mg. of vitamin in 100 gm. of dried grass/mg. of vitamin in 100 gm. of medium for half-maximum growth.

and valine. All of these amino acids of *Spartina*, when calculated according to methods of Mitchell and Block (1946), show more than 60 per cent deficits when compared with the corresponding contents of amino acids of beef muscle and fish muscle (Table 7). Of course, such calculations may have nutritional significance only when "the composition represents the pattern of amino acids which are absorbed into the animal" following digestive and other preparatory processes (Allison 1949).

If marine animals resemble the rat and man with regard to requirements for essential amino acids in normal growth and maintenance, then the question arises concerning the source of adequate protein feedstuffs in the sea. In addition to marsh grass, the second source of primary food in the coastal waters of Georgia is the phytoplankton diatoms and flagellates. According to the compiled data of Walford and Wilber (1955), diatoms are lower in arginine than marsh grass, but somewhat higher in histidine, and

about ten times as high in tryptophan. Although the available data are too few, still the indications are that high quality protein may not be formed by either marsh grass or phytoplankton. There remains the unexplored possibility that microbial conversion may act like a huge transformer to step up the potential value of the pool of protein in the sea. Examination of the data available for non-marine *Lactobacillus*, *Bacillus* and *Escherichia* (Lugg 1949) indicates that their per cent composition of the essential amino acids is higher than in *Spartina*. It appears worthwhile to pursue further studies on the physiological activities of bacteria that are known

TABLE 7. *Deviation*[6] *in per cent of amino acids of No. 3 Spartina sample below or above the amino acids in proteins of beef, fish and average Gramineae. (Data from Block, 1945; Lugg, 1949).*

Amino Acids	Deviation from Beef Muscle	Deviation from Fish Muscle	Deviation from average Gramineae
Arginine	−79	−78	−90
Leucine	−75	−73	−56
Isoleucine	−80	−79	
Lysine	−16	−24	+ 7
Methionine	−89	−90	−76
Phenylalanine	−77	−75	−55
Tryptophane	−41	−41	−60
Histidine	−91	−63	−93
Valine	−77	−77	−60
Threonine	−51	−50	−24

[6] Per cent deviation $= \frac{x - y}{y} \cdot 100$, where x is the amino acid of one protein (*Spartina*) and y is the corresponding amino acid of another protein (beef, etc.), the values of x and y being given in gm. per 100 gm. of protein, based upon N = 16 per cent.

to grow upon marsh grass and planktonic residues in the marine environment.

SUMMARY

1. Samples of young, and mature, leafy shoots, and weathered stems of the marsh grass *Spartina alterniflora* Loisel. were collected, from marsh regions along the coast of Georgia, for proximate analyses, and for the determinations of ten B vitamins and ten essential amino acids.

2. Proximate analysis of young *Spartina* yields values similar to those which have been published for Coastal Bermuda grass. The following data (per cent dry basis) represent the contents of growing shoots of *Spartina:* fat, 2.98; protein, 13.24; crude fibre, 29.75; ash, 12.83; and nitrogen-free extract, 40.20. The therms per pound are 1.68.

3. Weathered shoots, collected in August from growth of the preceding year, show loss of their leaves, and greatly lowered content of fat, protein, calcium and phosphorus.

4. The B vitamins, in general, appear to be present in adequate amounts

for growth of guinea pigs, as is indicated by comparison of the vitamin level in the dried grass and in experimental rations. The B vitamins are present in sufficient amounts for growth of heterotrophic microorganisms.

5. The ten essential amino acids, required for growth of the rat and man, constitute about 15 per cent of the protein of *Spartina*. Biological value of the protein is calculated to be deficient as a nitrogen supply for marine animals, and it is suggested that microbial conversion of the grass may act as a transformer to step up the potential value of the pool of protein in the sea.

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SOME GRASS GENERA WITH LIQUID ENDOSPERM[1]

WILLIAM G. DORE

On reading Walter V. Brown's report on the liquid condition of the endosperm in *Limnodea arkansana* (Brown 1955), I immediately went to the herbarium to check specimens of that species and compare the condition with that in some other grasses in which I thought it also occurred, namely *Koeleria cristata*, *Trisetum spicatum* and *Sphenopholis intermedia*. When the presence of an identical condition was confirmed, the examination of grains was extended to other species in the same and related genera.

The following species were found to have liquid endosperm:

Koeleria
- *cristata* (L.) Pers.
- *phleoides* (Vill.) Pers.
- *pyramidata* (Lam.) Domin
- *villosa* Pers.

Trisetum
- *bifidum* Ohwi
- *canescens* Buckl.
- *cernuum* Trin.
- *flavescens* (L.) Beauv.
- *melicoides* (Michx.) Vasey in Scribn.
- *spicatum* (L.) Richt.
- *subalpestre* (Hartm.) Neum.
- *wolfii* Vasey

Sphenopholis
- *filiformis* (Chapm.) Scribn.
- *intermedia* (Rydb.) Rydb.
- *obtusata* (Michx.) Scribn.

Helictotrichon
- *hookeri* (Scribn.) Henrard
- *planiculmis* (Schrad.) Pilger
- *pratense* (L.) Pilger

Additional species in the same genera are represented in the Departmental herbarium but most specimens were found to have been collected in too immature a stage of development to allow determination of the in-

[1] Contribution No. 1526 from the Botany and Plant Pathology Division, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

ternal nature of the caryopsis. A survey of ripe specimens in other herbaria would undoubtedly complement and extend the list. The representation of species in the four genera as listed above, however, seems sufficiently large and the occurrence of liquid endosperm sufficiently consistent in them to allow one to conclude that liquid endosperm is a character of whole genera rather than of individual species.

The genera *Koeleria, Trisetum, Sphenopholis* and *Helictotrichcon* are now placed by most authors in Tribe Aveneae, and Hitchcock, in 1920, placed them contiguously in this sequence, the last named genus at that time being included in *Avena*. The currently accepted separation of *Helictotrichon* from *Avena* is further justified by the difference in their endosperms.

To determine if liquid endosperm was prevalent throughout Tribe Aveneae, representative species of other genera placed at one time or another within it were examined. In the following species the mature caryopsis was found to be hard and its endosperm dry and "mealy": *Schismus arabicus* Nees, *Deschampsia caespitosa* (L.) Beauv., *Aira caryophyllea* L., *Corynephorus canescens* (L.) Beauv., *Avena fatua* L., *Arrhenatherum elatius* (L.) Presl, *Holcus lanatus* L., *Sieglingia decumbens* (L.) Bernh., *Danthonia spicata* (L.) Beauv., *Hierochloë odorata* (L.) Beauv., *Anthoxanthum odoratum* L. The character therefore does not apply to the whole Tribe as presently or formerly constituted.

Limnodea arkansana, belonging to a monotypic genus, is placed by Hitchcock (1920) in Tribe Agrostideae, positioned between *Cinna* and *Alopecurus*. It is interesting to find that Martin (1946) listed these three genera among seven having endosperm "soft-fleshy in consistency": *Limnodea, Koeleria, Holcus, Sphenopholis, Cinna, Beckmannia* and *Alopecurus*. Representative specimens of *Cinna, Beckmannia* and *Alopecurus*, the genera not covered already in the discussion, were then examined. In *Cinna latifolia, C. arundinacea, Alopecurus aequalis* and *A. pratensis* the endosperm may be fairly described as "soft-fleshy", not liquid as in *Limnodea*. In other genera of Tribe Agrostideae, eg. *Agrostis, Calamagrostis, Phleum* and *Muhlenbergia*, the endosperm is typically firm and mealy. In *Beckmannia syzigachne* of Tribe Chlorideae, the endosperm is soft-fleshy.

It is likely, then, that the liquid character is not always a clear-cut one, and critical judgment (or some more objective measure) will have to be used to assess it properly for purposes of phylogeny. Particular care will be needed when older herbarium specimens are being examined since, after 30 or 40 years, the endospermic material tends to become less fluid, loses its "watery" reflective surface, and develops a consistency which could be described as plastic, pasty or soft-fleshy. It should be mentioned too, that the liquid condition found in fully ripe grains of those grasses which possess it should not be confused with the "milk stage" of developing grains which,

in fresh material, it resembles; caryopses dried while in the milk stage collapse and shrivel.

Judging from the available literature, I am inclined to agree with Brown (1955) that the character of liquid endosperm has been generally overlooked by students of the grasses. Its significance in evolutionary studies and its value in delimiting genera and tribes cannot be fully decided until a comprehensive survey of genera has been undertaken and its incidence correlated with other taxonomic features.

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EPIPHYLLOUS FLOWERS

HARVEY E. STORK[1]

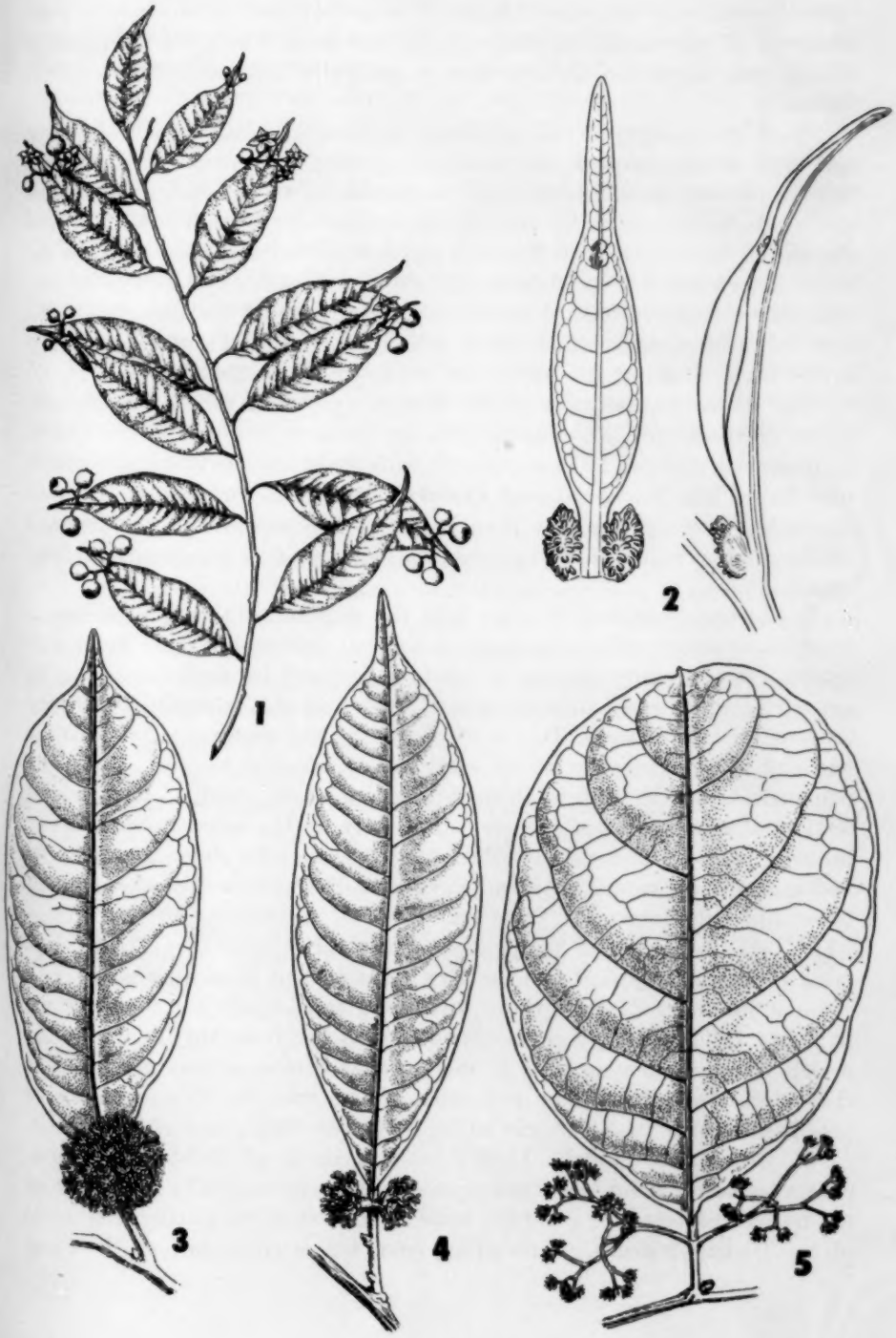
Phyllonoma ruscifolia Willd. is a species of small trees occurring occasionally in the montane forests of Central America. The species was established by Willdenow in 1820 and is included in the Family Saxifragaceae by most taxonomists. Some eight or ten other species have been described from Mexico to Northern South America but the distinctions are rather meager in some of these.

In 1928 the writer collected specimens from three trees of 20 to 25 feet in the mountains of Central Costa Rica, on the second ridge south of the city of Cartago, at an elevation of 7800 feet The trees were very conspicuous because of flowers and fruit occurring on what were regarded as cladophylls that bore a striking resemblance to true leaves. Later investigation proved them to be true leaves, so recognized by Leavitt (1909) who based his judgment on the studies of M. Casimir DeCandolle (1890).

A number of botanists expressed skepticism when I referred to these structures as true leaves. They cautioned that one is easily deceived by the close similarity between many cladophylls and leaves. It was also suggested that if they were true leaves there might be a concrescence of the axis of the inflorescence with the petiole and midrib. The writer therefore revisited the mountains south of Cartago in 1952 in order to fix tissues of developing leaves so that the origin of the inflorescences might be studied. The original trees had been destroyed by Podocarpus logging and it required some four days of search to locate four other plants,—an indication that the species is not very successful. One may also surmise that this is the case from the fact that very few specimens of the genus are found in some of the larger herbaria in spite of the striking anomalous appearance of flowers and fruits on leaves, a character that might catch the eye of the general collector. The trees are elements of the second story

[1] The author is grateful to Sigma Xi-RESA for assistance in collecting material.

FIG. 1. A shoot of *Phyllonoma ruscifolia* Willd. ×½. FIG. 2. Early stage of development of the leaf of *Phyllonoma ruscifolia* showing the beginning of the inflorescence on the midrib. Stipules with glandular hairs are seen at the base. ×6. FIG. 3. Leaf and inflorescence of *Gonypetalum tessmannii* Krause. Drawn from herbarium material collected in Dept. Loreto, Peru. Herbarium of the University of California, Berkeley. ×¾. FIG. 4. Leaf and inflorescence of *Tapura capitulifera* Baill. Drawn from University of California Herbarium material. Collected in State of Amazonas, near mouth of Rio Embira. ×¾. FIG. 5. Leaf and inflorescence of *Dichapetalum Spruceanum* Baill. Drawn from herbarium material collected in Dept. San Martin, Peru. From University of California, Berkeley, Herbarium. ×¾.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of the forest. None exceeded 3 inches in stem diameter. Of the several trees observed all were not completely shaded but stood where the overarching canopy was somewhat thinner than is generally the case in this upland forest.

Since the growth of the main axis is continuous, all stages of flower and fruit development may be found at any time. Though numerous berries were produced, no seedlings could be found on the ground. The flowers are produced in a cyme on the adaxial surface of the midrib well toward the tip of the mature leaf. Flowers and mature berries may occur on the same inflorescence or infruitescence. From this point the lamina is considerably attenuated toward the pointed apex. Some of the leaves show the start of inflorescences which abort before reaching any differentiation of flower buds. Some of the leaves are sterile from the first.

The leaves bear stipules which develop early and fall before the maturity of the leaves. They do not become foliar in shape, but are irregularly-shaped masses of tissue covered with numerous multicellular glandular hairs. The leaves subtend axillary buds which produce no inflorescences but may develop into branch shoots. The presence of stipules and axillary buds would seem to establish the true leaf character of these organs.

It has been surmised by some that the position of the inflorescence is brought about by the early coalition of the embryo leaf and floral axis tissues. The thinking here is probably influenced by such conditions as prevail in the bracted inflorescence of *Tilia* and the probable coalescence in some Dichapetalaceae. This is disproved by the presence of an axillary bud and by the character of the early development of the leaf. When the primordium of the leaf is about 4 mm. in length, median longitudinal sections show a region of greater cell activity on the adaxial side midway between the base and the tip. The subepidermal cells show larger nuclei and a deeper staining cytoplasm. Periclinal divisions in the subepidermal layer and enlargement of these cells produce a swelling on the surface which is the beginning of the primordium of the inflorescence. Its development proceeds in typical fashion. Proliferation and branching result in a cyme of several to fifteen flowers, presenting at maturity the aspect shown in figure 1. The supplying vascular strands arise from the bundle of the midrib in the same manner as do those that lead to secondary veins. Below the inflorescence there is no indication of two vascular strands, either in petiole or midrib, such as might be expected were this a case of coalescence.

M. Casimir DeCandolle (1890) made a study of leaf-borne inflorescences, some of which occurred occasionally or sporadically and some as the normal pattern. He regarded some of his examples, particularly some of the Dichapetalaceae, as resulting from the concrescence of the floral

axis with the leaf. Most of his study was on herbarium material. He however had living material of a cultivated ornamental species of the Cornaceae, *Helwingia japonica* Dietr., and concluded that in this case the inflorescences arose on true leaves in the same manner as if they had originated from stem tissue. Likewise, a study of *Phyllonoma ruscifolia* Willd. represented only by herbarium specimens led him to regard this as a similar case. Clearly indicated here is the need of morphogenetic studies of the various cases of epiphyllous flowers in some widely separated families. A superficial look at herbarium specimens of some of the Dichapetalaceae leads one to believe that they represent concrescence, but judgment must await morphogenetic studies. Drawings from herbarium sheets of three representatives of this family are shown in figures 3 to 5.

The phenomenon of flowers that take their origin in the meristem of true leaves must be taken into consideration in any generalizations on the fundamental difference between stem and leaf and on the evolutionary history of these organs.

SUMMARY

1. *Phyllonoma ruscifolia* produces its flowers and fruits in cymes that are outgrowths from the midribs of true leaves.

2. Morphogenetic studies show that the primordium of an inflorescence arises from the leaf meristem and that there is no coalescence between a floral axis and the leaf. The leaves bear stipules and subtend axillary buds.

3. This condition corresponds to that of *Helwingia japonica*, but probably not to leaf-borne inflorescences of the Dichapetalaceae where various degrees of coalescence prevail.

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MATERIALS FOR A DICTIONARY OF BOTANICAL TERMS—IV. TERMS TO DESCRIBE APICES[1]

H. W. RICKETT

The terms used for the apices of leaves, capsules, anthers, and other parts of plants are of great importance in descriptive botany; the apices of leaves are of special importance in diagnosis. It may therefore occasion some surprise that present and past usage of some of these terms has been neither precise nor uniform.

Such words as *acutus, obtusus, attenuatus* were first used botanically in their literal meanings as these were understood by those who wrote Latin in the middle ages and subsequently. But, in an effort towards precision, one meaning had to be chosen from the several attached to a single word; and rather general words, such as *acutus*, had to be sharpened to a greater precision. The genius of Linnaeus was evident in this direction as in others; but even he could not always be consistent; and those who followed him often seem to have varied the meanings of words to suit their fancy. A glance at the various illustrations of a single term (figs. 3 and 8) will substantiate this statement; it is as true of some of the moderns as of the ancients. Of course it is always possible to say, as some do: this is the way the term is used *in my book;* and so to attain a sort of temporary precision. But, aside from the desirability of such a subjective attitude towards terminology, authors cannot always be trusted to stick to their own definitions, or to use them consistently.[2] There is really no substitute for general acceptance of a term in a precisely stated meaning.

In approaching the apices of leaves one must first decide what the "point" or "tip" is. Such expressions as "sharp-pointed" or "tipped with a short, rigid point" convey no precise information about the shape. How long is a point, and how sharp? Such questions may have meaning to a connoisseur of ancient weapons, but none to a botanist. A point is defined by the intersection of two lines. An angle is measured by fractions of the circumference of a circle. In applying such concepts to the description of leaves, we must admit that the extremity of a leaf is never a mathematical

[1] Previous papers in this series have appeared in Bull. Torrey Club **81**: 1–15, 188–198 (1954); **82**: 419–445 (1956).

[2] In fact, what is "acuminate" to one may be "cuspidate" to another; while several such terms may be defined by one author in almost the same words and illustrated by almost the same figures, so that he may apparently use sometimes one and sometimes another to describe the same sort of apex. Such a procedure is scarcely conducive to the progress of science.

point, and that its margins are never straight lines; its sharpness is a matter of degree. But so are all our measurements, in physics as in botany; and we can approach precision in our descriptions only by setting up a precise standard with which to compare them.

Some botanists apply terms as they recognize species, by a sort of feeling for the totality rather than by analysis. The trouble with this is that the feeling is difficult to impart to others. If we want precision in our descriptive terms for the shape of the terminal part of a leaf, for instance, we must, as far as possible, define it in terms of the relation between the lines traced by the margins as they approach the extremity; and we must separate from this over-all shape the character of the extremity itself. A leaf may be quite obviously acute or acuminate but either rounded or sharp at the extremity (fig. 9); both facts must be stated to convey the picture accurately.

It is on this basis that I venture to offer not only an analysis of past and present usage of certain terms but proposals for a resolution of certain conflicts. A similar attempt will be made in a following installment on terms descriptive of bases of leaves and other parts.[3]

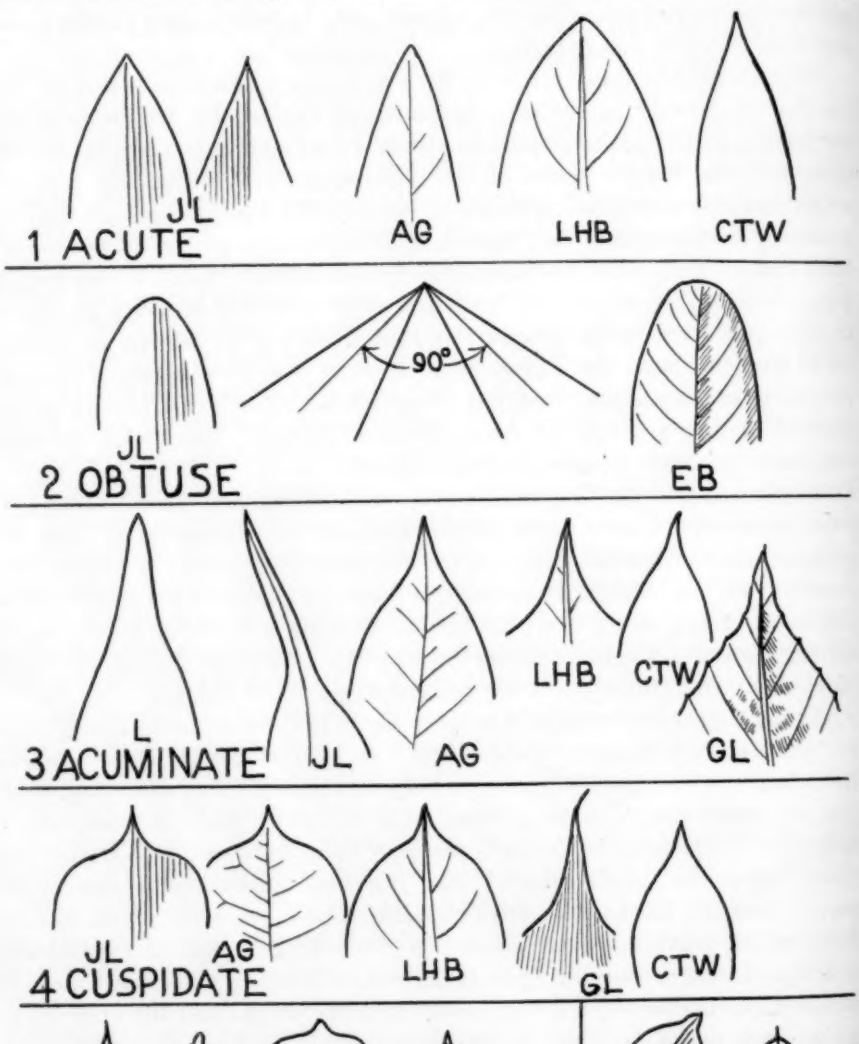
Acute and **Obtuse**. In a general way these words have served to separate most leaves (for which parts they have been principally used) into two groups: those which are sharp at the end and those which are blunt. Presumably they are thought of not only as mutually exclusive but as exhaustive (all leaves being either sharp or blunt). But the distinction is not easy to specify. How blunt is blunt? Does it mean lacking a point altogether? Or do we mean by an "obtuse" leaf one pointed by an obtuse angle?

Etymology does not help. *Acutus* in Latin is the past participle of *acuo*, to "sharpen"; it means "made sharp," and refers primarily to weapons, secondarily to the senses, etc.; the underlying reference is to something which cuts or penetrates, a concept applicable to some thorns but scarcely to most leaves. *Obtusus* is similarly derived from *obtundo*, to "strike, beat upon," hence to "make blunt," etc. The two words express exactly opposite concepts; but the causative element in each (to *make* sharp, to *make* dull), which provides a clear separation of meaning as applied, for instance, to weapons, has no bearing upon their botanical use. We are not concerned with sharpening leaves, but with leaves that *are* sharp; and the question remains: how sharp?

Many botanists have defined an "acute" leaf simply as "sharp", "sharp-pointed," or the like (WW, GWB, EB, B & B, AR), or as ending in an "acute angle" (L, JBB, DC, SFG, GB, HAG,); but a number have striven towards greater precision. Though to JHB, GB "acute" meant "terminat-

[3] The drawings in the accompanying figures are not photographic or mechanical reproductions but are faithfully copied, to the best of my ability, from the illustrations of the authors cited. Though some may question such a method, I think it has adequately preserved the intent of those who made the original drawings.

ing gradually in a sharp point'' (i.e. probably one formed by concave sides; this is the shape of the figure given for a definition by CTW—see figure 1),



FIGS. 1–6. Drawings to illustrate shapes of leaf apices, copied from the illustrations of the authors cited by initials.

most have taken it as formed by straight or slightly convex lines, as JP ("abruptly"), JL, AG ("without much tapering"), AC, BDJ ("not drawn out"), JCW ("tapering in straight lines"), LHB ("the sides of the tapered apex essentially straight or slightly convex"), GL; see figure 1. R & F, MLF call it a "well-defined angle," which allows plenty of scope. But even those who have defined it more vaguely have actually distinguished "acute" from "acuminate" in their writing and in their figures. An angle, of course *must* taper, since the area bounded by the sides must diminish in width as one approaches the point of intersection; but it is clear that for most of these authors "acute" referred to apices formed by straight or nearly straight margins. Since the general outline of a leaf (other than linear or subulate leaves) is almost necessarily formed by convex lines, such a concept of "acute" excludes apices terminated by an abrupt point (e.g. a mucro; see below), that is, a point formed by lines which change from convex to concave, or change direction in a distinct angle. Although, etymologically speaking, such apices are really acute, to use the word botanically in such a wide sense would rob it of most of its usefulness to botanists and would leave them without a word especially reserved for a common type of apex. The best characterization of "acute" would seem to be one which expresses more clearly the concept at which the authors cited above seem to have been aiming: a figure formed by lines which are nearly straight or convex and do not noticeably change their direction or their curvature.

"Obtuse" has often been defined merely as "blunt" (WW, AG 1848, EB, CTW, HAG); or as "rounded" (L, DC, SFG, JL, AC, JCW, LHB, GL). Many have "blunt or rounded," which implies a certain meaning for "blunt" (GWB, AG 1864, GB, R & F, B & B, BDJ, MLF). Only JBB, GWB, GB speak definitely of an obtuse angle. The dictionaries define the word mostly by negation, as "not acute"; which admits of a wide range of meanings. The same term is, then, used by botanists variously to describe two distinct kinds of apex: "blunt-pointed" (i.e. obtuse-angled in the mathematical sense) and "rounded." Merely to say "blunt" may mean either or both of these. The preponderance of usage seems to favor "rounded"; yet I suspect that many of the authors who so define it in their glossaries would actually describe the bluntly angled leaves of *Nyssa biflora* shown in figure 9, *c, d*, as "obtuse" and use "rounded" for that at *e* and for such a leaf as that of *Caltha palustris*. Indeed HAG says "rounded *or* obtuse" of the leaves of *Nyssa biflora*, *Viola odorata*, *Asclepias sullivantii*, and other species, clearly implying that his "blunt" *at least sometimes* means "blunt-pointed" rather than "rounded." If, on the other hand, we insist that "obtuse" and "rounded" are equivalent terms, then either we have two words for one shape and none for the other; or else, as seems generally the case, a loose use of "obtuse" in varying senses.

If we reserve "obtuse" for "obtusely angled," leaving "rounded" for tips that do not end in an angle, then how can we differentiate "obtuse" from "acute"? Mathematically an acute angle is less than 90°, an obtuse angle between this and 180° (see fig. 2). It is to be hoped that botanists, at long last, will be agreeable to using such a distinction in the interests of precision and intelligibility; it should not be difficult to apply. Bearing in mind the separation made above between the over-all shape of the apex and the character of the extremity, we may determine the acuteness or obtuseness of a leaf by drawing straight lines along the converging sides; the method is illustrated in figure 9. The leaves at *a* and *b* are, by this standard, "acute"; those at *c* and *d* "obtuse"; that at *e* "rounded." However, since nature is not always precise or uniform, it must be recognized that the leaf at *a*, whose extremity is definitely "blunt," might be spoken of as "rounded" rather than "acute." Such intergrading conditions may be described by hyphenation (a device familiar to systematists), as, for instance, "rounded-acute." Other types may be distinguished as "sharply acute," or "bluntly acute" (as at *b*).

We may notice in passing that SFG limited the use of "obtuse" to "the top," which seems inconvenient and unnecessary.

Acuminate and **Attenuate**. *Acuminatus* in Latin is from *acumino*, to "make pointed"; itself derived from *acumen*, a "point"; this contains the root AK, seen also in *acuo* and many other words, signifying a "point." *Attenuatus* is the past participle of *attenuo*, to "make thin," etc.; it means "made thin" (as an adjective it had various derived meanings, as "weakened," still seen in the English "attenuated"). Since to make a thing pointed also involves making it thin, at least at the end, it is clear that there is likely to be some overlapping in the use of these terms; and overlapping there has been.

To L "acuminatum" meant "[folium] quod terminatur apice subulato." "Subulatus" meant "linear and narrowed at the apex," not "awl-shaped"; being applied to flat bodies. "Attenuatus" does not appear among his terms. By some of his contemporaries and by some recent authors "acuminate" is defined in such a way that it means no more than "acute": WW ("tapering to a point"), JP, EB, R & F, B & B, BDJ, AR, HAG, CD, WD, OED; unless we are to assume some other meaning for "tapering" than that given in the dictionaries ("diminishing in breadth towards one end"). It is probable, however, that all or most of these authorities did intend something more than "acute," something even more than "narrowly acute" by their definitions. Their "tapering," by several qualified as "gradually tapering," probably implied a change in the direction of curvature from convex to concave, so that the *rate at which the apex diminishes* in breadth lessens as one approaches the end. The same concept is probably implied by the words

"prolonged" or "drawn out" ("allongée", "ausgehend") used by JBB, DC, GWB, AG, JHB, AC. That this interpretation of past usage is correct is borne out not only by the few definitions that attain some degree of precision, but also by the figures of JL, WW, AG, and that used as a definition by CTW (see fig. 3). SFG has "the two edges change their direction when they approach each other, and are prolonged beyond the place where they would otherwise meet." GB approaches the same concept in less clear language: "when suddenly narrowed near the top, and then more or less prolonged into an *acumen* . . ." JCW has "tapering to a point in hollow curves," and LHB, followed by GL, refers it to "an acute apex whose sides are somewhat concave and taper to a protracted point" (see fig. 3). It is curious that so few recent authors have followed the example set so long ago by SFG. A modern definition of "acuminate" may read: applied to an apex bounded by lines or surfaces which change from straight or convex to concave and converge gradually towards a point (cf. mucronate, cuspidate, below). It should be noticed that the apex of the process so formed may itself be acute, obtuse, or even rounded. The word *acumen*, it is true, suggests something sharp; but if we do not widen the sense, as with "acute," to include various types of extremities, we shall have to substitute several new terms for "acuminate"—which would seem unnecessary and confusing. As here defined, acuminate" may often describe too short and too abrupt an apex to satisfy the feelings of some modern botanists. I suggest that the precision inherent in the concept is worth some sacrifice of personal feelings; and that qualification, as "short-" or "long-acuminate," may differentiate the various types of apices that fall under the definition.

"Attenuate" has been generally taken in its literal meaning of "tapering," variously qualified as "tapering gradually to a point", "slenderly tapering," and so forth. In short, WW, JP, AC, R & F, BDJ, AR, MLF, HAG make no evident distinction between "acuminate" and "attenuate"; some use the same words for both definitions. Some of the older authors, including L, do not define *attenŭatŭs*, doubtless seeing it as simply a Latin word without special botanical meaning. SFG defined it as "becoming narrow at bottom"; and LHB, with GL, has "applied to bases or apices." GWB limited it to solid (terete) parts, reserving "angustatus" for flat bodies; but in this he has not been generally followed. It is questionable whether the term has any special meaning. If it means "tapering gradually with straight or slightly convex sides," then we may use "narrowly acute" with a better prospect of making ourselves clear; and this may be said of apices or bases. If it refers to a gradual taper with concave sides, then it duplicates "acuminate" for apices. Its usefulness may lie in its literal sense of "narrowed," or "tapering," without reference to apices. A body may be "attenuate" in either direction and still "obtuse" or "rounded."

Mucronate, Cuspidate, Apiculate. Such definitions as "sharp-pointed" (WW, JP), "finishing in a narrow point" (SFG), "possessing a short and straight point" (BDJ), "tipped with a short, sharp, slender point" (HAG) give little information on the exact form which they seek to designate; for a "point" is necessarily rather sharp and slender, and has no length. When we insert the word "abrupt" in the definition we begin to have some conception of what is meant: "tipped with an abrupt slender point" (AG 1848), "tipped with a short abrupt point" (AR), "with a short, sharp abrupt tip" (B & B), and so on (JL, JHB, EB, R & F, LHB, MLF, GL, OED, WD, CD). Some express the same idea by such phrases as "when the midrib is produced beyond the apex in the form of a small point" (GWB, GB). We must therefore assume, in reading all the above definitions, that they refer to a tip or point whose sides make a definite angle with the margins of the leaf or other part; otherwise we can get no precise meaning at all for the terms.

The above-cited definitions were all applied to "mucronate." Those of "cuspidate" are similar: "terminé par une pointe sétacée et un peu roide" (JBB), "spit-pointed" (WW), "tipped with a sharp and rigid point" (AG 1864), "with an apex somewhat abruptly and sharply concavely constricted into an elongated sharp-pointed tip" (LHB, GL), "with a cusp" which is "a sharp, abrupt, and often rigid point" (HAG). No clear difference between "mucronate" and "cuspidate" appears in these definitions; indeed the two are synonymous according to CD, and LHB has almost identical figures to illustrate them (see figs. 4, 5). There is, however, a greater assortment of varying concepts for the latter word than for the former (see fig. 4). To SFG it meant "long, narrowing by degrees, ending in a sharp hard point resembling awlshape leaves, but much larger"; to JL "tapering gradually into a rigid point"; and similar ideas are expressed by GWB, JHB, CTW. In such senses the word is equivalent to "acuminate," with "stiffness" added. Such a concept has disappeared from most modern glossaries. Since this earlier meaning practically duplicates "acuminate" and the later interpretation is indistinguishable from that of "mucronate," the term "cuspidate" should probably be abandoned.

Etymologically *mucro* is a "sharp point," e.g. of a sword; *mucronatus*, "pointed," is literally much the same as *acutus*. *Cuspis* is the "point" of a spear, a "spit," or a "sting"; *cuspido* is to "sharpen"; *cuspidatus* is literally provided with a sort of needle-like rather than with a flat point. But this difference would be difficult to apply and seems not to have taken part in the botanical history of the word.

There have been similar divergences in the meaning of "apiculate." The modern Latin word *apiculus* is a diminutive of *apex*, meaning only a "little point." JL says "apiculate" differs from "mucronate" "in the point being

part of the limb, and not arising wholly from a costa" (fig. 6). To AR it is "contracted into a minute point" (so also AG 1848). CTW has "with a small broad point at the apex." to HAG it is only "usually" sharp, while to BDJ and GL it is "sharp and short, but not stiff" and "short, sharp, flexible"; to JHB "soft." Several authors indeed seem to make the lack of rigidity a distinguishing feature (EB had the mucro also a "small, soft point"; but he was alone in this). The lack of unanimity, and the frequent difficulty in knowing whether a minute tip is rigid or soft (if minute enough it is almost certainly *somewhat* rigid) make such a distinction of doubtful use. SFG had a fairly clear separation of these three terms: a mucro to him was stiff, straight; a cusp long and needle-like; an apiculus short, hair-like, and not stiff. But to follow him, setting at naught all the varying ideas that have intervened, would be difficult—even if it would work with the plants themselves. In my opinion precision of description would be best served by getting rid of "apiculate" with "cuspidate" and using "mucronate," with suitable qualifying words, for any abrupt point short of "aristate" or "caudate."

It should be noted that for short abrupt points of terete parts we have "rostrate" and its diminutive.

Aristate, awned. From the Latin *aristatus*, itself derived from *arista*, the "beard" of an ear of grain, and hence the "ear" itself. *Aristatus* was used classically in the sense of "provided with ears of corn," but in the botanical Latin of the 18th century and onward it meant "provided with a beard"; from this it has come to mean "provided with a stiffish bristle-shaped appendage" (R & F) or "tapered to a very narrow much elongated apex" (LHB), referring not only to grasses but to plants of any family.

The word "beard" itself has long been in common use for awns, "singly or collectively," as AC says, in the Gramineae; it may mean one awn (JL, AG 1864, LHB, GL), or all the awns of an ear (WD). The latter would seem to be a more natural application of a common English word, which generally signifies more than one hair or bristle. Botanists have also used "bearded" in various other senses more akin to its ordinary English meaning, as "hairy in some parts and not in others" (SFG), "beset with bristly hairs" (AG 1848), "bearing tufts, spots, or lines of hairs" (AG 1864); and most recent authors give alternate meanings (R & F, BDJ, AR, OED, CD, GL). To some, however, a "beard" refers only to long stiff hairs (MLF, WD, LHB); GL is almost alone in keeping alive the old meaning of a "tuft" of hairs. Several authors have confusingly defined "beard" to mean an awn but "bearded" to refer to a type of pubescence (JL, AG 1864).

Obviously, since "beard" is often equivalent to "arista," and "bearded" at least sometimes to "aristate," all these terms need clarification. In the past an arista has been provided with not only various but conflicting defini-

tions. Compare the following: "poil roide ou de pointe filiforme terminal ou dorsal qui ne semble pas être la continuation d'une nervure" (DC; SFG has almost the same); "a hard, straight, subulate point of various lengths. The arista is always a continuation of the costa" (JL). To GWB it was a continuation of a nerve in many grasses but not in other plants. To some it is a bristle-like appendage (MLF, BDJ); by others it is applied also to a tapered point (LHB); and many are not explicit on this point. The most general definition of "aristate" today is "tipped by a bristle" (AR); but we must eliminate from our definitions the reference to a terminal attachment (GL, HAG), since this excludes the awns or aristae of many grasses. JL defined "aristate" as "terminated . . ." but his figure shows a dorsal awn. Furthermore, a "bristle" is generally thought of as terete, and "aristate" should not, therefore, be applied to a clearly flattened tip no matter how prolonged. We need only clear statement here to make the term useful; and "bearded" *in this sense* should be abandoned in botanical writing, to avoid giving it two meanings of which one duplicates "aristate."

Caudate. From the Latin *cauda*, a "tail"; *caudatus* is modern Latin meaning "having a tail"; and so most botanists have defined it. It came in, apparently, with SFG, who used it of an "appendage like a tail" on anthers or follicles. Previously WW and DC had introduced *cauda* to botanical terminology, DC in the sense of an "appendice terminal quelconque, long, mol, flexible et semblable à la queue d'un animal." JL said of the adjective "excessively acuminated . . ."; he applied it to sepals and petals. Since his time, definitions of "caudate" have been less satisfying. "Having a (slender) tail-like appendage" (R & F, B & B, MLF, WD) does not inform us what sort of a tail is meant (boxer or poodle) nor to which end of the creature it is considered to be attached. LHB exemplifies it by "spadices of some aroids," and GL adds "some leaf apices," thus finally giving some exactitude to its application. OED refers to certain fern fronds, and CD to "seeds or other organs which have such an appendage."

Evidently, "caudate" may refer to leaves, fruits, anthers, floral envelopes, seeds, or any other parts which bear a long, slender, terminal appendage which may be likened to a tail. Since tails are rarely stiff, and since awns are, a *cauda* may be understood to be more or less flexible, as far as plants are concerned; at least it is not setiform. From the wide range of its applications, it may be either terete or flattened. It is a useful term for a very protracted leaf apex, and JL's "excessively acuminated" is about as good a definition as any.

Retuse and **Emarginate**. For "retuse" L has "[folium] quod terminatur sinu obtuso"; for "emarginate", "quod terminatur crena." A *sinus* in Latin was the "fold of a garment," hence the "bosom," finally a "bay" or "gulf": essentially a curve. A *crena* was an "incision" or "notch":

FIGS. 7 and 8. Drawings to illustrate the terms *retuse* and *emarginate* as represented by the authors cited by initials. The contrasting definitions of each author are arranged vertically; the evolution of the term may be read horizontally.

essentially an angle. The two terms are thus clearly separated, as they apply to the apices of leaves, one meaning indented by a rounded depression and the other by a sharp incision. Curiously, L's figures seem to be just reversed (figs. 7, 8); and this, which I take to have been an accident, may have been the origin of the ensuing confusion of the terms. The situation is further complicated by the presence in L's plate of an entirely different shape called *emarginatum acute;* while his figure of *retusum* has no very definite apex, but shows a leaf notched all around (crenate). *Retusus* is from *retundo* and means only "blunted." It might apply to rounded or truncate leaves, or, as WW says, to one that is "dented." *Emarginatus* is the past participle of *emargino,* to "take away the edge"; to cut a notch is one way to "take away the edge," and it must have been in such a sense that L adopted it. A notched razor, for example, is generally regarded as dulled.

On the definition of "emarginate" there is substantial unanimity; it means "notched at the apex." WW, who usually adhered closely to L, substituted the latter's figure of *fissum* for his "emarginate," besides copying the curious split-acuminate tip called *emarginatum acute;* either figure illustrates an apical notch. But for "retuse" there has always been a choice of meanings (fig. 7). JBB, who contrasts "sinus" with "angle," follows L in his view of "retuse": "terminé par un sinus obtus." So also, from their figures, JCW and CTW, and probably JHB ("slightly depressed") and EB ("a broad shallow sinus"); perhaps also SFG ("ending in a blunt notch"). OED, CD agree that a sinus is a rounded depression, and define "retuse" in the same terms (but CD's figure has a notch). But to DC a sinus was an angle (though his definition of "retuse" is "écrasé"); and it might be either rounded or acute to GWB (who preferred "rounded"), AG 1864, AC, JCW, BDJ, R & F, MLF, WD. Others from JL to HAG do not specify the shape of the sinus and are probably to be included with the last; since "sinus rounded" and "sinus acute" are frequent diagnostic phrases, e.g. for the leaves of *Acer*. Accordingly almost all these authors define "retuse" as "notched." LHB, indeed, uses almost the same words for "retuse" and "emarginate"; and GL, following his definitions as usual, has new figures which almost reverse the orginal meanings (figs. 7, 8). JP has "bitten off"; perhaps confusing "retuse" with "premorse," which was applied by L to the notched end of a leaf of *Liriodendron*. AG 1848 has a "round notch," whatever that may be. Most of the others, including all recent authors, have "shallowly" or "slightly" notched. Several (AG 1864, GB) distinguish "retuse" as less "decidedly" (deeply?) notched than "emarginate." Some of the figures are sufficiently bizarre to suggest that their authors had to draw something to illustrate a definition for which they had no real use.

The use of "retuse" in almost the same sense as "emarginate" leaves the shape originally designated by the former word nameless (except, per-

haps, in England, where the transfer seems not to have occurred). Though to restore the original meaning would seem desirable on both sides of the Atlantic, it may be impracticable. Perhaps it is worth trying. Certainly we do not need both terms as currently defined in America, and, since "retuse" is open to question, let us either abandon it or reinstate it as "with a rounded sinus at the apex."

FIG. 9. Leaves of *Nyssa biflora*.

Truncate. From the Latin *truncatus*, past participle of *trunco*, to "lop" or "maim"; it meant "lopped off", "mutilated", "deprived of." L used it in the sense of a leaf "quod linea transversali desinit," in which meaning it has been generally adopted by botanists. L included it among the terms descriptive of the apex of a leaf. He was followed closely by almost all the authors here cited. GWB broadened the concept to include solids as well as flat surfaces, in which OED is careful to concur. Of my authors LHB was first to apply it to "base or apex"; he is followed by GL and HAG; but surely there must have been others who *used* the term for the base of a leaf

even while they defined it in the restricted Linnaean sense. There is little need to discuss the various definitions given, though some are interesting. WW, in his usual laconic fashion, says simply "lopped." DC has "il semble qu'on a coupé un morceau," which lacks the precision usual with this master of terminology. JBB regards "truncatus" and "praemorsus" as equivalent, and JCW defines the former as "with broad straight end, as if bitten off." There seems no reason why the word should not be used of bases as well as apices; it is as useful at one end as at the other; but certain problems arise which will be discussed in a later installment of this series, in a consideration of terms applied to bases.

Premorse. This, from the Latin *praemorsus,* participle of *praemordeo,* to "bite in front," to "take away," and meaning "bitten off," is certainly one of the most amusing terms foisted upon an unwary science by the sometimes pawky progenitor of its terminology. He applied it to a leaf "quod obtusissimum terminatur incisuris inaequalibus" and illustrated it with a leaf of *Liriodendron tulipifera* (of a rather unusual form, having deep lateral sinuses, but the usual widely notched end). This may be disconcerting to some of our modern writers, who apply it only to rhizomes of *Viola* and *Hieracium* (JHB, HAG, R & F, MLF); these would seem to have little in common with the said leaf. Many have defined it in what they must have taken to be the literal sense of "bitten off." The trouble is that the shape of something bitten may vary with the kind of jaw that does the biting. Compare a horse's bite with a dog's, for instance; or are we to assume that these various parts of plants appear as if bitten off by a man, or a child? Some qualify the definition to accord better with L's original meaning and to separate it from "truncate" and other shapes: they say "rogné" (JBB, DC), "ragged and irregular" (JL, WD, CD) or "as if the end had been chewed or bitten off" (LHB, GL). Many authors omit it from their glossaries, and this, in my opinion, is the proper thing to do with it.

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A STUDY OF THE THREE-DIMENSIONAL CONFIGURATIONS OF SPOROGENOUS CELLS IN THE ANTHERS OF TRILLIUM ERECTUM L. WITH SPECIAL REFERENCE TO THE GEOMETRICAL ASPECTS OF CELL SHAPE[1]

JOAN ELMA RAHN

Cell shape studies in the past have been concerned with both morphologically differentiated and undifferentiated tissues. Among the latter, many have been apical meristems and the tissues immediately derived from them. With the exception of coconut endosperm (Seigerman 1951), of the development of which little is known, no study of a mass meristem has yet been made from this standpoint. With the increasing realization that the direction of cell division plays an important role in cell shape determination, it seemed desirable to study such a meristem.

Among mass meristems are classified the reproductive tissues producing spores and sperms, endosperms, certain apical meristems, and some stages of young embryos (Esau 1953). The last two seemed the least suitable, for they exhibit few meristematic cells along any diameter. Therefore an effort was made to find a sporogenous tissue which could be utilized. Genera from all the major groups of the plant kingdom were considered. Sporogenous cells of algae and fungi for the most part are too small for this type of analysis. Since an homogeneous tissue was desired, liverworts, in which elaters are associated with the spores, were eliminated. Furthermore, since cells in the two outermost layers should not be used in a study of this type, it was essential that the material selected have at least five cells across its narrowest dimension, and preferably more. This resulted in the elimination of many mosses, ferns, and angiosperms.

Sporangia from a variety of plants which met the requirements outlined above were sectioned and stained. In many cases the dense cytoplasm of the sporogenous cells took up the stains to such an extent that it was impossible to follow the cell walls. The plant finally selected was *Trillium erectum* L., which has large anthers several mm. long. Although there is considerable variation, the four microsporangia often show six or more microspore mother cells along the diameter of a transverse section.

Material and methods. Rhizomes of *Trillium erectum* were purchased in September from the Gardens of the Blue Ridge, N.C. The stages in the

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development of the anther have been closely timed (Sparrow and Sparrow 1949). In September the sporogenous cells are in pre-meiotic interphase or early meiotic prophase I. At that time no rounding up has occurred, no intercellular spaces are present, and the cells are essentially isodiametric. The rhizomes were packed in peat moss and kept in a refrigerator for one month at approximately 4°C. At this temperature meiosis occurs so slowly that over a period of several weeks the cells are still in prophase I. All cells utilized in this study were in interphase or early leptotene.

Stamens were removed from the buds and immediately killed and fixed in Craf and dehydrated by an ethyl alcohol-xylol schedule and embedded in a 50:50 mixture of paraffin and Tissuemat. Both transverse and longitudinal sections were made at 50 μ. Most of the slides were stained in ruthenium red (12 hours) and fast green (3 minutes), a few with a modification of Foster's (1934) schedule combined with Feulgen. When viewed with an orange filter the cell walls stood out sharply; the large nuclei were visible, but did not interefere with the clarity of the cell walls.

Cells to be studied were picked essentially at random. However, only cells separated from the tapetum by at least two sporogenous cells were used. Since the divisions in the anthers are essentially synchronous, dividing cells were rare, but on the few occasions in which they were found, the area about such cells was avoided.

The cells were studied under oil immersion at a magnification of 970 diameters. Upper and lower contacts were first drawn by plotting all corners with the aid of a camera lucida and connecting them with straight lines. The sides were drawn in similar fashion with repeated focusing up and down. The reading on the fine adjustment scale of the microscope was recorded for each corner. No effort was made to record the curvatures of the walls. The drawings represented an approximate magnification of 1800 diameters. The cells were taken from eight anthers in seven flower buds from four rhizomes.

Data. The 100 cells ranged from 9-hedra to 21-hedra, the average being 14.65 ± 0.23 (table 1). The most common were 14-hedra (20 per cent), next 13-hedra (16 per cent) and 15-hedra (15 per cent). Ninety-two combinations were found (table 2); 41 of them have not been reported before in plant tissues; 47 are new among morphologically undifferentiated cells. Only two cells showed identical arrangement of faces. The commonest combination had 3 quadrilaterals, 7 pentagons, 2 hexagons and 1 heptagon (3-7-2-1) and was present in three cells. The two identical cells had the formula 4-4-4. Five other combinations were found two times each: $\overset{\Delta}{2}$-4-2-1-4, 3-6-4, 5-3-4-1, $\overset{\Delta}{1}$-4-5-3-2-1, 3-7-5-1. No tetrahedral angles were found.

The faces ranged from triangles to decagons (table 1), the most com-

mon being pentagons (34.3 per cent), the next, quadrilaterals (25.8 per cent), and then hexagons (21.0 per cent). An unusually high percentage of triangles occurred—5.3 per cent.

TABLE 1. *Number and kinds of faces in 100 sporogenous cells in the anther of Trillium erectum.*

No. of faces	No. of cells	Total faces	Kinds of faces	Total faces	% of total
9	1	9	Triangular	77	5.3
10	2	20	Quadrilateral	378	25.8
11	3	33	Pentagonal	503	34.3
12	10	120	Hexagonal	308	21.0
13	16	208	Heptagonal	128	8.7
14	20	280	Octagonal	55	3.8
15	15	225	Nonagonal	12	0.8
16	12	192	Decagonal	4	0.3
17	10	170		1465	
18	4	72			
19	5	95			
20	1	20			
21	1	21			
	100	1465			

$$\text{Average} = \frac{1465}{100} = 14.65 \pm 0.23$$

Discussion. These data present an unusual situation. Extremes never before reported for tissues essentially undifferentiated morphologically are in evidence here. The average of 14.65 faces per cell is high—significantly over 14.0, sometimes postulated as the "ideal". It exceeds all averages recorded for morphologically undifferentiated tissues, the previous range having extended from 13.36 in *Eupatorium* pith (Marvin 1939) to 14.48 in coconut endosperm (Seigerman 1951). Most of these averages in tissues previously analyzed have been somewhat below 14.0.

Hulbary (1948) used the criterion of approximately 85 per cent of the cells lying within the 12- to 16-hedron range as being indicative of an homogeneous tissue. The present cells do not meet this criterion, only 73 per cent lying within that range, and 86 per cent lying within the 11- to 17-hedron range. The possibility is suggested that the tissue is not an homogeneous one. A tissue composed of large and small cells such as *Eupatorium* pith presents a wide range of cell types with a relatively small percentage of the cells lying within the 12- to 16-hedron range. Marvin reported only 69 per cent in that range. Mixed aggregations of compressed lead shot (Matzke 1939) or of bubbles (Matzke 1945, Matzke and Nestler 1946) of different volumes likewise showed low percentages in that range. The *Trillium* tissue, however, is composed of cells of nearly equal volume. Furthermore the high average number of faces per cell argues against the non-homogeneity of the tissue. Aggregations of cells, of compressed lead

TABLE 2. *Ninety-two combinations of faces in 100 sporogenous cells of Trillium erectum.*

Total faces	Number of sides per face								No. of cells
	3	4	5	6	7	8	9	10	
9		4	4	1					1
10		4	4	2					1
10		5	2	3					1
11	1	2	6	1	1				1
11	2	1	5	2	1				1
11		5	3	2	1				1
12	1	1	8	1	1				1
12	1	2	6	2	1				1
12	1	3	4	3	1				1
12	1	4	3	2	2				1
12	2	2	5	1	1	1			1
12		4	4	4					2[a]
12		4	5	2	1				1
12		5	2	5					1
12		5	3	3	1				1
13	1	2	6	3	1				1
13	1	2	7	2	0	1			1
13	1	3	5	3	0	1			1
13	1	4	4	2	1	1			1
13	2	4	2	1	4				2
13	3	3	1	2	4				1
13		3	6	4					2
13		3	7	2	1				3
13		5	3	4	1				2
13		5	4	2	2				1
13		6	3	2	1	1			1
14	1	2	7	2	2				1
14	1	2	8	1	1	1			1
14	1	3	5	3	2				1
14	1	3	6	2	1	1			1
14	1	4	5	1	2	1			1
14	1	4	5	2	1	0	1		1
14	1	5	2	3	3				1
14	1	6	2	2	1	2			1
14	2	3	2	6	0	1			1
14	2	3	3	4	1	1			1
14	2	3	4	3	0	2			1
14	2	3	5	1	1	2			1
14	2	5	2	1	2	2			1
14		2	8	4					1
14		2	9	2	1				1
14		3	6	5					1
14		4	5	4	1				1
14		4	6	2	2				1
14		5	4	4	0	1			1
14		6	3	2	3				1
15	1	2	7	3	2				1
15	1	3	6	3	1	1			1
15	1	4	5	1	4				1
15	1	5	3	3	2	1			1
15	2	4	3	3	1	2			1
15	2	4	3	3	2	0	1		1

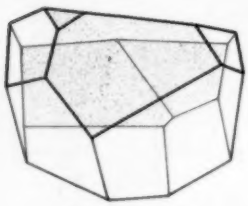
TABLE 2—Continued

Total faces	Number of sides per face								No. of cells
	3	4	5	6	7	8	9	10	
15		2	8	5					1
15		3	7	4	1				1
15		3	8	3	0	1			1
15		4	5	5	1				1
15		4	6	3	2				1
15		4	6	4	0	1			1
15		5	5	3	1	1			1
15		6	3	4	1	1			1
15		6	4	3	0	2			1
16	1	4	5	3	2	1			2
16	1	4	6	2	2	0	1		1
16	1	5	4	4	0	1	1		1
16	2	4	4	2	3	0	1		1
16	2	4	5	1	2	1	1		1
16		2	9	4	1				1
16		3	7	5	1				2
16		3	8	4	0	1			1
16		4	6	5	0	1			1
16		5	6	3	0	2			1
17	1	3	6	5	1	1			1
17	1	3	7	3	2	1			1
17	1	4	3	8	0	1			1
17	2	2	6	4	2	1			1
17	2	5	4	2	1	2	1		1
17	3	3	4	3	2	1	1		1
17	5	3	1	4	1	1	1	1	1
17		4	5	7	1				1
17		5	5	5	1	1			1
17		6	5	2	3	1			1
18	1	4	6	5	1	0	0	1	1
18	1	6	4	2	4	0	1		1
18		5	6	4	2	1			1
18		6	4	5	2	1			1
19	1	4	6	5	1	2			1
19	1	4	7	4	2	0	0	1	1
19	1	5	7	1	3	1	1		1
19	2	5	3	3	5	1			1
19		3	10	3	2	1			1
20		4	9	5	0	1	1		1
21	1	5	6	5	3	0	0	1	1
Totals	77	378	503	308	128	55	12	4	100

[a] These two cells had identical arrangement of faces.

shot, or of bubbles tend to have a lower average number of contacts per unit when the units vary in size than when they are of equal volume.

Several other features correlated with those already mentioned, but at first glance perhaps more obviously correlated with each other, are the distribution of types of faces and the numbers of combinations of the



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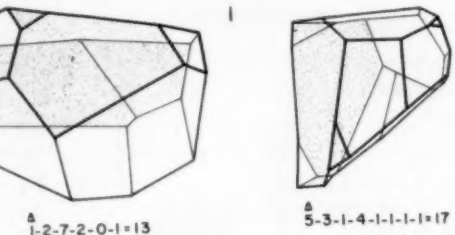

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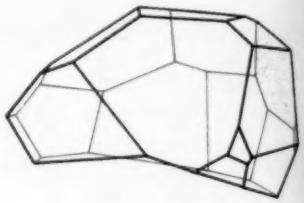


7

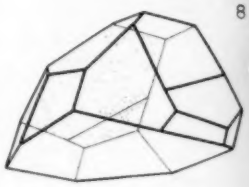
A 1-2-7-2-0-1=13

A 5-3-1-4-1-1-1-1=17

4-9-5-0-1-1=20

1A

4A



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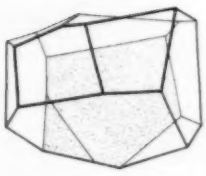

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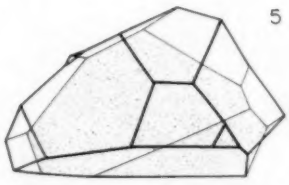

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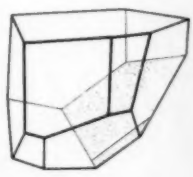

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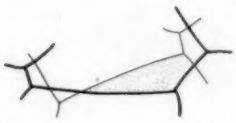
A 1-3-5-3-0-1=13

A 2-4-4-2-3-0-1=16

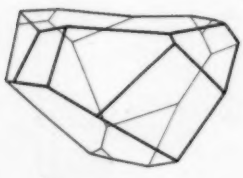
4-4-4=12

2A



5A

10



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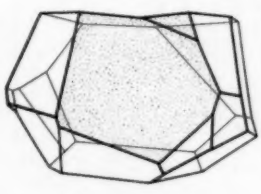
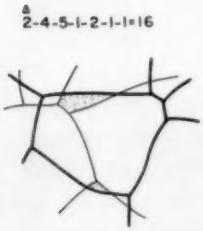


6

A 2-2-6-4-2-1=17

A 2-4-5-1-2-1-1=16

A 1-4-6-5-1-2=19



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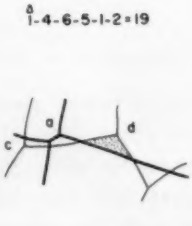
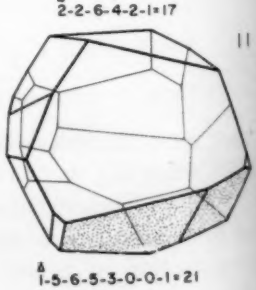


6A



11

A 1-5-6-5-3-0-0-1=21

faces. Sporogenous tissue of *Trillium* had 11 per cent of its cells composed of only quadrilaterals, pentagons, and hexagons—the lowest figure thus far reported for morphologically undifferentiated tissues. Triangles, heptagons, octagons, and larger faces were more numerous than in other tissues. The wide range of face types made possible the occurrence of 92 combinations —the highest number to be demonstrated in morphologically undifferentiated tissues. Since there were almost as many combinations as cells, it is obvious that most of them could occur only once—85 were found only once —again the highest number reported for such a tissue.

FIGS. 1–11. Camera lucida drawings of 11 cells, slightly schematized to avoid superimposition of corners and edges. The shaded faces are those which form dihedral angles of 175° or greater. ×900. FIG. 1. A 13-hedral cell with an octagonal face perpendicular to the adjacent faces, which include a triangle and a large hexagon in one plane, and a quadrilateral and a pentagon in one plane. FIG. 2. A 13-hedral cell with an octagonal face perpendicular to the adjacent faces which include a triangle and a large hexagon in one plane, and a wedge-shaped quadrilateral. FIG. 3. A 16-hedral cell with an octagon and a nonagon, each perpendicular to its adjacent faces, the former adjacent to a triangle, the latter adjacent to a triangle and several other small faces. FIG. 4. A 17-hedral cell, with a nonagon and a decagon each perpendicular to its adjacent faces, many of which are triangles and other small faces. A triangle and an octagon lie in one plane. This cell has five triangles, the largest number found in any of the 100 cells studied. FIG. 5. A 16-hedral cell with a nonagon perpendicular to its adjacent faces which include a wedge-shaped quadrilateral and a heptagon in one plane (lower surface) and a triangle and three other small quardrilaterals. The smaller triangle and a heptagon on the upper surface are also in one plane; these are not shaded. FIG. 6. A 19-hedral cell with an octagon perpendicular to its adjacent faces, which include a triangle and an octagon in one plane. FIG. 7. A 20-hedral cell with a nonagon perpendicular to the adjacent faces. A hexagon and a small quadrilateral lie in one plane. FIG. 8. A 15-hedral cell with an octagon perpendicular to the adjacent faces which include several small faces. A small quadrilateral and a large hexagon lie in one plane. FIG. 9. A 12-hedral cell with a pentagon and a small quadrilateral in one plane. FIG. 10. A 17-hedral cell with a triangle and an octagon in one plane. FIG. 11. A 21-hedral cell with a decagonal face perpendicular to some of the adjacent faces. Two pentagons lie in the same plane. This cell had the largest number of faces in the 100 cells studied. FIGS. 1A–6A. Camera lucida drawings of criss-crossed divisions giving rise to many of the small wedge-shaped faces in the cells illustrated in figures 1–6. The small wedge-shaped faces which are shaded are those found in the cells in figures 1–6. The larger faces of these cells and the faces of adjacent cells are not shaded. The shading of figs. 1A–6A does not correspond with the shading of figures 1–6. In most cases the small faces alternate in position on either side of the division walls. ×600. FIG. 1A. Origin of the wedge-shaped quadrilateral on the lower surface of the cell in figure 1. An adjacent cell has a similar face. FIG. 2A. Origin of the triangle and the wedge-shaped quadrilateral on the lower surface of the cell in figure 2. The small triangle and the pentagon are in an adjacent cell. These small faces alternate in position on either side of the dividing walls. FIG. 3A. Origin of the triangle and the wedge-shaped quadrilateral on the lower surface of the cell in figure 3. Adjacent cells each have a triangular face. FIG. 4A. Origin of three triangles and one quadrilateral on the lower surface of the cell in figure 4. Adjacent cells have received two triangles and two quadrilaterals. FIG. 5A. Origin of the wedge-shaped quadrilateral on the lower surface of the cell in figure 5. There is a triangular face in an adjacent cell. FIG. 6A. Origin of the triangle on the upper surface of the cell in figure 6. A triangle and a small wedge-shaped quadrilateral are in an adjacent cell.

The importance of the direction of division in determining the number of combinations has been noted in the past. Higinbotham (1942) and Dodd (1944) reported 69 and 65 combinations in 100 cells each, in the undifferentiated cells in the petiole of *Angiopteris* and in the carpel vesicles of *Citrus*, respectively. These tissues showed divisions in several directions. Duffy (1951) noted that there were more combinations in the initial region of tomato roots, where divisions were in all directions, than in other regions studied. The 99 combinations of 125 coconut endosperm cells were ascribed to criss-crossed divisions by Seigerman. With the exception of tomato all of the tissues mentioned above as having a high number of combinations also had relatively few cells in the 12- to 16-hedron range. The previously mentioned *Eupatorium* pith (Marvin 1939) had 61 combinations among the 100 cells. It thus appears that irregular tilting of the cell plate may produce some data similar to those achieved by the irregularity of cell size.

Randomly oriented divisions, characteristic of mass meristems, may easily produce criss-crossed divisions. Features so unusual for undifferentiated cells (high average number of faces per cell, high percentages of triangles, heptagons, octagons, and larger faces, and large number of combinations), but present in the sporogenous tissue of *Trillium*, may be correlated with criss-crossed divisions as shown by Wheeler (1955). Such divisions were immediately obvious upon examination of the *Trillium* tissue. There was no evidence that any "slipping" had occurred. Cells with faces produced by criss-crossed divisions are illustrated in figures 1–6. Figures 1A–6A show the origin of some of these faces by such divisions.

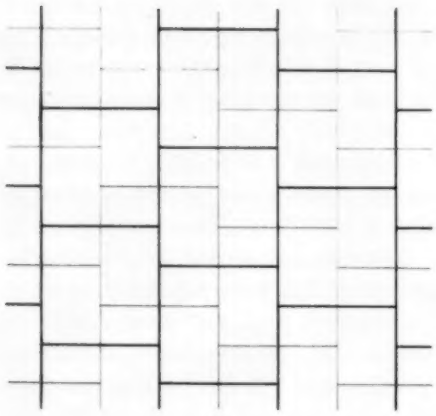
Tissues averaging considerably higher than 14.65 contacts per cell have been reported. These for the most part consisted of cells morphologically differentiated. Lewis (1935) explained the high average observed in pine tracheids as being due to the bending of the cells and the resulting overlapping of their ends. He furthermore showed how these could be derived from 14-hedra. Dodd (1948) studied the cambium of pine, and found an average of 18 contacts per cell, but since 4 of the 18 were with small ray initials, an average of 14 may be obtained by discounting the latter. Wheeler (1955) demonstrated an average of 15.4 for cambium cells in *Aloe*. Dividing cork cambium cells and cork cells produced by cork cambium cells which have not undergone an anticlinal division showed averages of 14.92 and 14.72 respectively in *Pelargonium* (Lier 1952). However, these were selected cells, and when data from other cork cambium cells and other cork cells were averaged in, the over-all averages dropped. Likewise, dividing cells in the meristem of *Anacharis* had an average of 16.84 contacts, but the apical meristem as a whole exhibited an average of 14.0 (Matzke and Duffy 1956).

Of five of the above tissues—sufficient data are not available for pine tracheids—all had less than 85 per cent of the cells lying within the 12- to 16-hedron range, four had a number of combinations equal to at least 70 per cent of the total number of cells, and most of them showed wide ranges of cell types and faces.

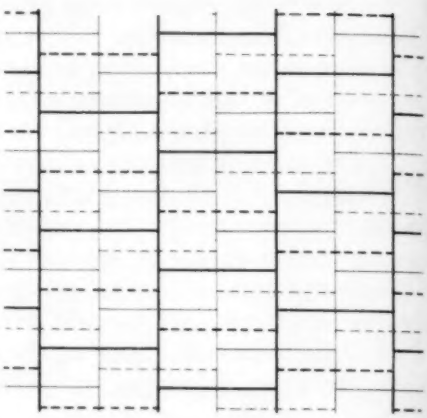
All of these tissues were composed of elongated cells and/or cells not surrounded by their own kind. Neither of these situations is applicable to the sporogenous cells in the anthers of *Trillium*. The problem then arises, is it possible to demonstrate a system composed of essentially isodiametric units or "cells" which partake of features usually evidenced by elongated cells and by cells not surrounded by their own kind? To make the system comparable to the situation in *Trillium*, there should be no intercellular spaces, no tetrahedral angles, and no four-rayed intersections.

Previous workers have made reference to the theoretical aspects of configurations of cells in a mass. In a footnote, Lewis (1928) pointed out that the division of a tetrakaidecahedron into two equal halves results in the addition of one new polyhedron and 14 new surfaces to an assemblage of polyhedra. The two daughter cells each have 11 faces or a total of 22. Assuming that the new wall is coincident with a hexagonal section of the tetrakaidecahedron one new face will be added to each of the six cells adjacent to that section. Subtracting the original 14 faces, $(22+6)-14$ equals 14. Meeuse (1942) presented a fuller discussion of this problem, and applied it to cells in mass meristems. He concluded that "in a mass meristem the number of contact faces, therefore, averages fourteen." In both cases it was assumed that the cell plate was hexagonal in outline. But it is obvious that if the plate is pentagonal or heptagonal fewer or more faces will be added. Lewis (1933) stated that "the total number of facets added to the mass by any division is twice the number of facets in the division plane plus two." While Lewis knew that the orientation of divisions could raise the average number of faces in a mass, yet he apparently did not believe that this actually did happen. There was reason for this, for by 1933 no tissue had been demonstrated to have an average significantly over 14. In the same paper he said that if such divisions did occur, there must be some compensating factor such as four-rayed intersections to keep the average at 14.

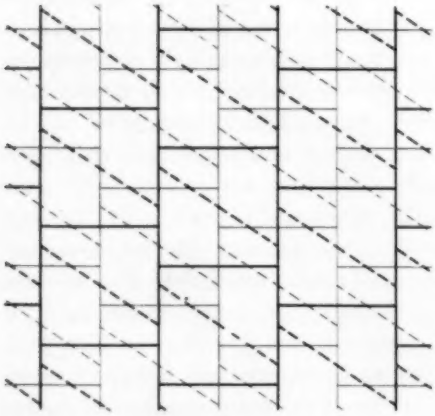
The relationship of the shape of the cell plate to the number of faces per cell may be expressed by the formula $t = 2x + 2$, in which t = total number of faces added by the division, and x = number of sides of the cell plate. Heptagonal cell plates will add 16 faces with each division, octagonal cell plates will add 18 faces, etc. The following discussion will show that a change in the orientation of the cell plate so that it is other than hex-



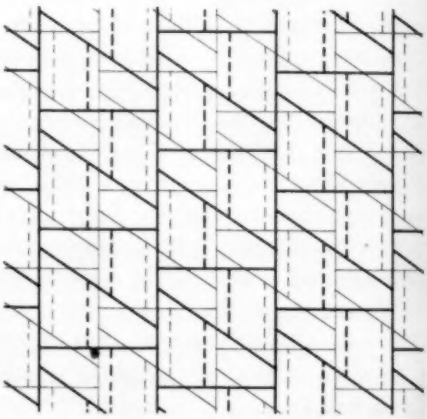
12



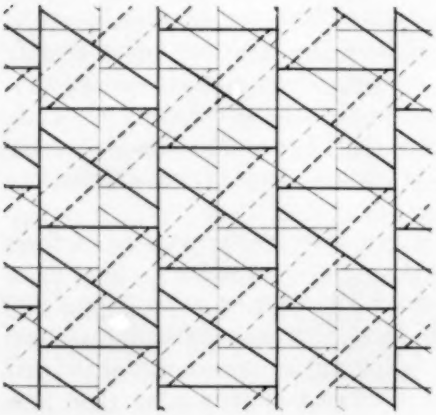
13



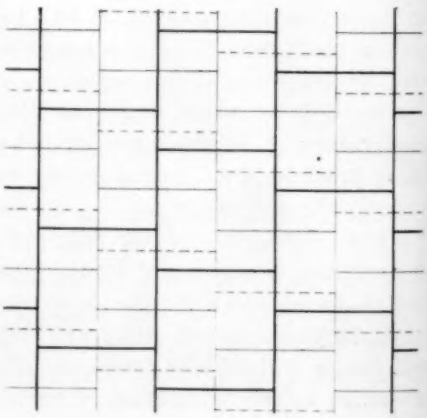
14



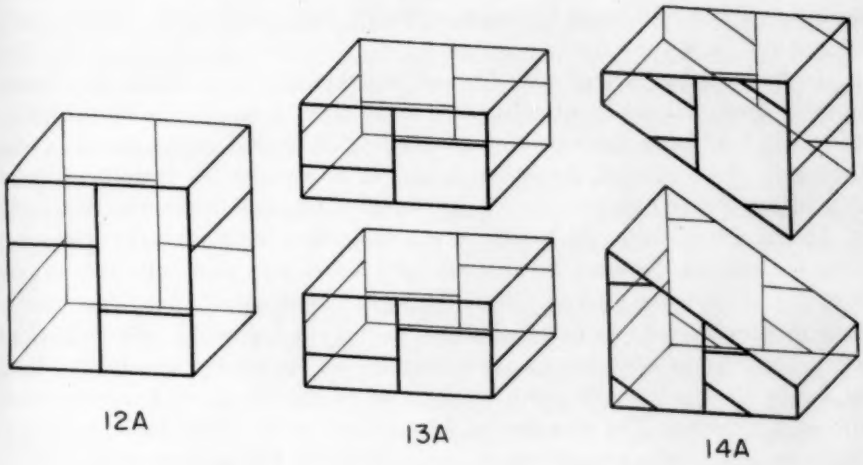
15



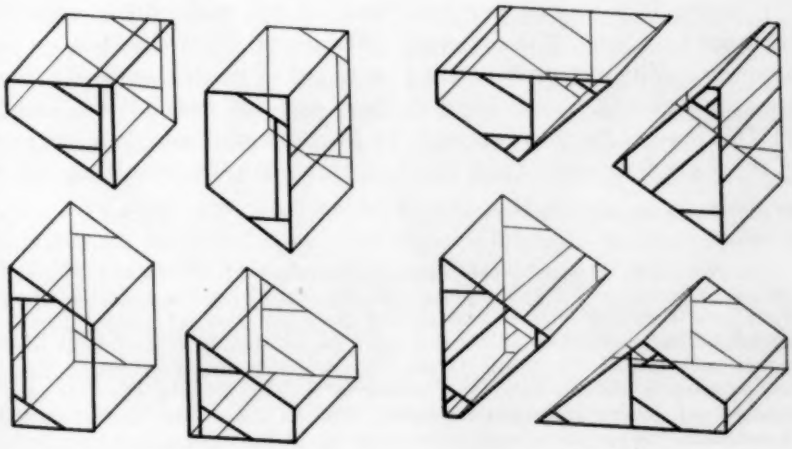
16



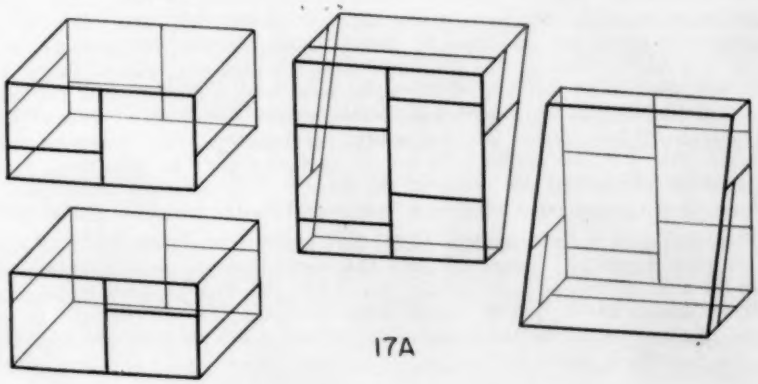
17



12A 13A 14A



15A 16A



17A

agonal in shape will cause a change in the average number of contacts from 14 per cell in a tissue.

In figure 12 a pattern of cells each surrounded by six cells was drawn in light lines. All are identical in size and shape. A similar pattern of cells drawn in bold lines was superimposed over this so that each cell made contact with four cells of the other layer. It is possible to imagine a mass consisting of any number of such layers piled on each other, the two types of layers alternating. Each cell is a tetrakaidecahedron, making contact with six cells in the same layer, four cells above and four cells below. One such cell is shown in perspective in fig. 12A. "Normally" in a rib meristem each new wall would be horizontal and would cut across six cell walls (two above, two below and one on each "side") as shown by the dashed lines in figure 13. Such a cell plate would add 14 new faces and one new cell for each division. The average of 14 contacts would thus be maintained. Two daughter cells are shown in perspective in figure 13A.

In figure 14 a dashed line was drawn across each cell to represent a criss-crossed division. The daughter cells are of equal size, but no longer isodiametric. The new wall is tilted so as to cut across ten walls (the cell plate is decagonal), thus adding 22 faces and one new cell for each division. This is eight faces in excess of the 14 required to maintain the average (or, there are four extra faces per daughter cell). The resulting cells each have 18 faces in the combination $\overset{\Delta}{8}$-2-0-4-0-0-0-4. Two daughter cells are

FIG. 12. "Cells" in a tetrakaidecahedral arrangement. Each cell of the layer drawn in bold lines is surrounded by six other cells. Below this layer is a similar one drawn in light lines. Each cell contacts four cells of the other layer. If a third layer similar to the second one is superimposed above, and a fourth similar to the first is placed below, then each cell of the middle layers will acquire four more contacts. These will have a total of 14 contacts each. Any number of these layers may alternate in a mass to produce any number of tetrakaidecahedra. FIG. 13. An "ideal" set of divisions in a rib meristem. The parent cells are drawn as in fig. 12. Each parent cell has divided into two equal halves. The hexagonal cell plates are indicated by dashed lines. See text for further description. FIG. 14. An illustration of criss-crossed divisions. The parent cells are drawn as in figure 12. Each parent cell has divided into two equal halves. The decagonal cell plates are indicated by dashed lines. See text for further description. FIG. 15. The parent cells of this illustration are the daughter cells of figure 14. Each parent cell has divided into two nearly equal masses by a quadrilateral cell plate. See text. FIG. 16. The parent cells of this illustration are the daughter cells of figure 14. Each parent cell has divided into two nearly equal masses by an octagonal cell plate. See text. FIG. 17. The parent cells are as in figure 12. The cells have divided by hexagonal cell plates. The cell plates of the layer in bold lines are nearly parallel with the plane of the paper and therefore do not appear in the illustration. See text.

FIGS. 12A–17A. Cells from figs. 12–17, here shown in perspective. FIG. 12A shows one cell from figure 12. FIGS. 13A and 14A each illustrate two daughter cells from figures 13 and 14, respectively. FIGS. 15A, 16A, and 17A each show four daughter cells from figures 15, 16, and 17, respectively. In figure 17A the two cells to the right are the daughter cells from the layer drawn in bold lines; the two cells to the left are from the underlying layer.

illustrated in figure 14A. Admittedly this is a highly artificial situation with an unusually high degree of regularity and the resulting cells show extreme characteristics not found in tissues. But it does demonstrate that a continuous system with more than 14 contacts can occur and illustrates how such a situation could arise. There is a large number of triangles and decagons—these account for ⅔ of the total number of faces. In *Trillium*, 18.8 per cent of the faces were other than quadrilaterals, pentagons, and hexagons. This is unusually high for a morphologically undifferentiated tissue.

Since a system averaging 18 contacts can be formed from one averaging 14, the question then arises: during subsequent divisions can an 18-faceted system maintain itself, or will it revert back to 14? Figures 15 and 16 show that either may happen depending on the orientation of the new cell walls. Daughter cells in these illustrations are of as nearly equal size as possible. In figure 15, the quadrilateral cell plates result in the addition of only 10 new walls and one new cell for each division. Each such division adds 8 faces fewer than necessary to maintain the average of 18 (or, 4 less per daughter cell). The daughter cells each have 14 contacts in the combination 6-0-8—the original condition has essentially been restored. Four of the daughter cells are seen in perspective in figure 15A.

If the average of 18 is to be maintained, then each division must bring with it 18 new faces. By the formula $t = 2x + 2$, it is obvious that this can be accomplished by an octagonal cell plate. Figure 16 shows criss-crossed divisions by means of 8-sided cell plates. The resulting cells average 18 contacts; half of the daughter cells have 17 contacts, half have 19. The system appears relatively irregular and there are two combinations—$\overset{\Delta}{6}$-2-2-2-0-4-0-1 and $\overset{\Delta}{6}$-2-2-4-0-4-0-1. Four of the daughter cells are drawn in perspective in figure 16A. Other averages may be obtained with other types of cell plates.

The fact that divisions are not all in the same direction does not necessarily result in the production of high averages. If no criss-crossed divisions occur and the cell plates are hexagonal, the resulting cells may have 14 contacts. Figures 17 and 17A illustrate such a system. The new cell walls of one layer are horizontal and hexagonal (fig. 17). The cells of the other layer (in bold lines) have divided in a plane nearly parallel with the paper, but the plane is tilted somewhat to avoid the meeting of four cells along an edge. Therefore these walls do not appear in figure 17, but they are indicated in figure 17A, and they are also hexagonal. The average number of contacts is 14. Two combinations are produced—5-2-5 and 4-4-8. Four daughter cells are shown in perspective in figure 17A. There is a narrow range of face types here, with only quadrilaterals, pentagons, and hexagons produced. This model, then, may be comparable

to the tissues studied by Hulbary, Dodd, and Duffy in which divisions were in more than one direction, and a large number of combinations occurred, but the average number of contacts per cell was close to 14. Figures 13–17 are summarized in table 3.

TABLE 3. *Summary of figs. 13–17.*

Figure no.	No. of faces per parent cell	No. of sides per cell plate	No. of faces added per division	Average no. faces per daughter cell	No. of daughter cell combinations	Combinations
13	14	6	14	14	1	6-0-8
14	14	10	22	18	1	Δ 8-2-0-4-0-0-0-4
15	18	4	10	14	1	6-0-8
16	18	8	18	18	2	Δ 6-2-2-2-0-4-0-1 Δ 6-2-2-4-0-4-0-1
17	14	6	14	14	2	5-2-5 4-4-8

The number of sides per cell plate is, therefore, one of the important factors in determining the number of contacts per cell. The number of sides varies somewhat, but in many tissues the average is probably near 6—the number required to keep an average of 14 contacts. Matzke and Duffy (1956) analyzed 75 late telophase cells in the stem apex of *Anacharis*. In these cells the cell plates had reached the walls of the parent cells, and the number of sides was determined. They found 9 pentagons, 48 hexagons, and 18 heptagons. The average was 6.12 sides. In *Anacharis* the cells of the apex are arranged to some extent in longitudinal rows, with the long axis of the cell parallel to the long axis of the stem. In transverse section the cells average 6 sides. The cell plates tend to be at right angles to the long axis of the stem and therefore are coincident with a transverse section. Thus the cell plates would be expected to average 6 sides. In all likelihood, this applies to other rib meristems and the tissues derived from them, though no analyses of such divisions have been made. The consistency of averages near 14 would indicate that such is the case.

In a mass meristem the situation is somewhat different. Schüepp (1926) characterized mass meristems as having either cuboidal or random divisions ("Würfel- oder Allwärtsteilung"). In the former case, the division "planes" are oriented with reference to three axes perpendicular to each other. In the latter case the cell plate of one cell seems to have no reference to the orientation of other cell plates (except to avoid tetrahedral angles)

or to any axis of the organ in which they occur. This is a characteristic of the *Trillium* tissue. The divisions are not entirely random, however. The cells are nearly equal in volume, and therefore the cell plate is most likely such that it divides the parent cell into two equal, or two nearly equal, masses. In 1952 Hull and Houk analyzed some of the possible planes that may intersect the orthic tetrakaidecahedron. These "cell plates" ranged from 3-sided to 10-sided. Though an average was not published, their graph showed a maximum at 6 sides, and the curve was such that the average must be near 6. Planes with fewer than 6 sides can divide the tetrakaidecahedron only into unequal parts. The figure may be divided equally only by 6-, 8- and 10-sided planes of intersection. If all tetrakaidecahedra in an aggregation divide with "cell plates" randomly oriented, except that the resulting "daughter cells" are equal in volume, then the "cell plates" must have 6 or more sides, and the average will have to be somewhat above 6. The average number of faces per "daughter cell" must then be greater than 14.

In the case of mass meristems a similar situation obtains. In the tissue here studied, the cells were all in prophase I and therefore it was not possible to determine with certainty the shape of the last cell plates. The faces ranged from triangles to decagons; therefore the cell plates were probably confined to the 3- to 10-sided range. Cell plates with only a few sides (triangles and quadrilaterals, especially) would have resulted in daughter cells of unequal size. Because of the irregular shapes of the cells, it is possible that 5-sided plates might occasionally have produced equal divisions, but the deletion of triangles, quadrilaterals and many of the pentagons as possibilities for the cell plates (since the cells were of nearly equal size), shifts the average to above 6 sides per cell plate. This would raise the average number of contacts per cell to above 14. According to the above formula a shift from 6 to 6.3 sides per cell plate will maintain an average of 14.65 faces per cell.

The prediction of Meeuse that mass meristems will average 14 contacts, then, can hold only if the divisions are oriented so that the cell plates average 6 sides. As shown above, this will not happen in the "Allwärtsteilung" type of meristem, if divisions produce cells of approximately equal volume. It may conceivably happen in the "Würfelteilung" type. If divisions are synchronous, and all cell plates are oriented in the same direction for any given set of divisions, then the cell plates would be expected to average 6 sides. The orientation of each set of cell plates at right angles to the previous two sets will not change this figure. This is the type of division discussed by Giesenhagen (1905) in the sporangia of *Botrychium Lunaria*. He described the division of one cell to form an "upper" and a "lower" cell, each of which divided to form a "left" and a "right" cell. Each of

these four cells divided to form a "front" and a "back" cell. Although he found this to be the usual pattern, exceptions were occasionally found. His illustrations show sister cells with cell plates oriented at right angles to each other. This change in orientation would cause some of the cell plates to cross each other with the resultant raising of the average number of sides per cell plate and the concomitant rise in the average number of contacts per cell.

Examination of the basic model of the 14-hedron system used as the basis for figures 12–17 brings another realization. These model cells, though having 14 faces each, are fundamentally cubes or rectangular prisms, much the same as bricks, which may be piled in such a fashion that each one contacts 14 others, but, when isolated, each brick has 6 faces. This model is not meant to imply that cells are fundamentally cubes or rectangular prisms, but rather to suggest that some pairs of faces, in a tissue of a high average number of contacts, may lie in the same plane, thereby making possible a situation in which a cell may be fundamentally a 14-hedron, while making contact with more than 14 cells. To simplify discussion, in the following paragraphs it will be assumed that all faces are planes, though this is not the case with actual cells.

Wheeler (1955) showed that the faces responsible for the high average number of contacts in *Aloe* cambium were triangles or other small faces, and these were frequently in contact with faces of 7 or more sides. Criss-crossed divisions were responsible for the production of these pairs of small and large faces. The new wall, for example, might cut across a hexagon, thus converting it into a heptagon. The triangle produced at the same time might abut on another hexagon and also convert it into a heptagon. Faces with more sides may likewise be produced. The cell illustrated in figure 6 has a triangular face which is adjacent to two octagons. The origin of this triangle by a criss-crossed division is suggested by figure 6A. In the absence of gliding growth, for which there is no evidence in this tissue, the triangle must have arisen by the crossing of the walls *ab* and *cd*. The two octagons, one in the same plane as the triangle, the other perpendicular to it, would most likely have been heptagons had the crossing of walls not occurred.

The most likely source of more than one face in a single plane would seem to be the two faces formed by the cell wall of an adjacent cell cutting across the original face. Since so many of the divisions in the *Trillium* tissue were criss-crossed, it was thought that perhaps some of these pairs containing the extra faces might lie in the same plane. Readings on the fine adjustment scale had been recorded for each corner when the original drawings were made. By utilizing these readings and taking into account the camera lucida magnification, it was possible to measure the dihedral

angles made by pairs of faces which lay in nearly the same plane. These included pairs of faces in which both members were nearly equal in size as well as pairs in which they varied greatly.

Pairs of faces were divided into three groups: the first in which the faces were in the same plane or made an angle of more than 180° (mostly 180° or slightly more), the second in which the faces made an angle of 175–180° and the third in which the faces made an angle of 170–175°.

TABLE 4. *Summary of the data pertaining to pairs of faces making dihedral angles of 170° or more.*

	Group 1	Group 2	Group 3	Original 100 cells
Range of dihedral angles	180° or more	175°–180°	170°–175°	
% of triangle-heptagon and triangle-octagon pairs	20.0	11.5	0	
% of triangles, heptagons and octagons	25.5	19.2	9.3	17.8
% of quadrilaterals, pentagons and hexagons	74.5	80.8	90.7	81.2
Average ratio of area of large to small face	20:1	8.8:1	2.7:1	

Pairs of faces involving quadrilaterals, pentagons and hexagons occurred most frequently in all groups. In the first group triangle-heptagon and triangle-octagon pairs accounted for 20.0 per cent of the pairs, in the second group, for 11.5 per cent, and in the third group for none. Triangles, heptagons and octagons comprised 25.5 per cent of the faces in the first group, 19.2 per cent of the second group and 9.3 per cent of the third group. These three types of faces accounted for 17.8 per cent of the faces in the tissue as a whole. Quadrilaterals, pentagons, and hexagons accounted for 74.5, 80.8 and 90.7 per cent of the faces in groups 1, 2 and 3 respectively, as compared with 81.2 per cent of the total faces for 100 cells (table 4). The shaded faces in figures 1, 2, 4–11 illustrate a few of the pairs of faces making angles greater than 175°.

It is obvious from this that with increase in size of the dihedral angle, there is an increase in the per cent of triangles, heptagons and octagons, and, conversely, a decrease in the per cent of quadrilaterals, pentagons and hexagons. Since the number of sides per face is roughly indicative of face area, this suggests that there is a tendency for small and large paired faces to lie in one plane, rather than faces of equal area.

Only 12 of the 77 triangles, 13 of the 128 heptagons, 5 of the 55

octagons and none of the nonagons or decagons present in the 100 cells were accounted for in the above pairs. Not all of such faces would be expected to contribute to paired faces. Every face is shared by two cells, and there is for each member of a pair, a corresponding face in one of two adjacent cells. Since the latter two faces are in separate cells they cannot be considered as a pair, although they also lie in one plane. This reduces by half, the number of triangles which might be expected to participate in pairing. This would lead one to expect about 38 triangles; roughly one third of these were realized.

Criss-crossed divisions usually produce two or more triangles, so arranged that some of the larger faces are adjacent to both of them. For this reason it is difficult to anticipate what fraction of the larger faces might be involved in pairing. It was obvious while making the original drawings of the cells that the largest faces were often nearly perpendicular to their adjacent faces (figs. 1–8, 11). This may account for the fact that no nonagons or decagons were involved. Many of these adjacent faces included pairs of large and small faces which lay in the same plane (figs. 1, 2, 4–6). Many of the large faces appeared to be the latest walls formed. Examination of figs. 14 and 16 will show that the new cell walls in the theoretical models have the highest number of sides and are perpendicular to the adjacent faces.

Wheeler (1955) further pointed out that all extra faces are not necessarily triangles, but they may be small wedge-shaped faces with a higher number of sides. With this in mind, comparisons were made among the three groups with reference to the ratio of areas of the two faces of each pair. The faces were reconstructed as accurately as possible in one plane. Again the corners were plotted by utilizing the readings on the fine adjustment scale, measuring the distances between corners on the original drawings, and correcting for camera lucida magnification. The corners were connected with straight lines, the areas of the reconstructed faces were measured with a planimeter, and the average ratio of area of the larger face of a pair to that of the smaller face was determined. In group 1 this ratio was 20:1; in group 2 it was 8.8:1; in group 3 it was 2.7:1 (table 4). These data, then, support the suggestion made above that there is a tendency for small and large faces to lie in one plane, for the larger the dihedral angle—i.e., the closer the dihedral angle is to 180°—the greater the ratio of the area of large to small face. Another indication that most of the pairs of faces are those resulting from criss-crossed divisions (and therefore including some of the extra faces) is the fact that the cells involved in the first group averaged 16.1 faces, those in groups 1 and 2 averaged 15.7 faces, and those in all three groups averaged 15.5. If each pair of faces is counted as a single face the average number of

faces for the 100 cells drops from 14.65 to 14.4 if only the first group is involved. It drops to 14.1 if the first and second are taken into consideration, and to 13.8 if all three are involved.

It might at first seem a valid argument that these pairs of faces lie in the same plane because they are the result of recent divisions of adjacent cells and therefore the cells have not had time to make the mutual adjustments which would cause the daughter faces to assume a more stable relation to each other. But there is no indication that all the pairs are the results of the last division. Indeed, if these pairs were the products of the last division it would be difficult to explain the differences among the three groups in ratios obtained for the areas of the pairs, for not all the faces cut by criss-crossed divisions are divided into unequal areas. Furthermore the anthers were killed and fixed one to two months after the last divisions occurred—a period of time during which any such adjustment might reasonably be expected to occur. Rather, there may be some mechanism which causes daughter faces of greatly unequal area to remain in the same plane as the parent face, whereas faces of nearly equal area may find a more stable arrangement by adjustments which produce a dihedral angle less than 180° between the daughter faces.

The tetrakaidecahedron with 14 faces in the combination 6-0-8 has long been discussed as a model or "ideal" for cells in tissues. One of the reasons for so considering it, is its great economy of surface. While extremely few cells are such tetrakaidecahedra, it cannot be denied that the averages of many tissues hover about 14 (Higinbotham 1942; Dodd 1944; Hulbary 1948; Duffy 1951; Matzke and Duffy 1955, 1956). This has been interpreted as a tendency toward economy of surface among cells. Bubbles in foams also approach this condition. Characteristics of foams are due largely to the action of surface forces. Uniform bubbles examined by Matzke (1945, 1946) showed an average of 13.7 contacts and had only four face types—quadrilaterals, pentagons, hexagons and heptagons. The high average number of contacts and the wide range of face types in *Trillium* are not indicative of stability or economy of surface. But the pairing of large and small faces may to some extent offset this feature. The pairing has two results. First it reduces the number of plane surfaces presented by a cell to approximately 14, thereby allowing the cell to approach more closely the surface-economy of the tetrakaidecahedra or of foams. Secondly the areas of plane surfaces are made more nearly uniform than would be the case if faces of equal area were so paired. Small faces are "eliminated" by adding them to large faces, the areas of which are not greatly increased by this addition. The tetrakaidecahedron is composed of two kinds of faces—quadrilaterals and hexagons. The abovementioned bubbles had only four types of faces and since the number of

sides per face is roughly indicative of face area the size of faces in bubbles is relatively uniform. The range of face size in *Trillium* is reduced by pairing, the faces become more uniform in size, and as a result the cells themselves become more uniform. In this respect the cells again are brought to resemble more closely both tetrakaidecahedra and foams.

The importance of the Kelvin tetrakaidecahedron should not be overemphasized. It certainly has features in common with cells of many tissues, or features which are approached by cells—the meeting of only three faces at a corner, the meeting of only three cells or polyhedra along an edge when stacked, economy of surface—and, of the wide range of geometrical possibilities, cells in tissues have utilized a comparatively few —mostly those which average close to 14 contacts. Yet the fact remains that the 6-0-8 combination has been realized only a few times in the wide range of tissues studied over a period of more than 30 years.

The results obtained in the anthers of *Trillium* will most likely find general applicability among mass meristems with random orientation of cell plates, and perhaps to some degree among those with more strictly oriented divisions. The former seem to provide a greater chance for the occurrence of criss-crossed divisions which result in the addition of extra faces to the cell mass and a wide range of cell types and of face types. The pairing of small and large faces in one plane, as found here, may or may not occur in other mass meristems. If this is a manifestation of a tendency toward stability among the cells, then its occurrence would be expected in other tissues of this type.

SUMMARY

1. An analysis of 100 sporogenous cells in the anther of *Trillium erectum* L. revealed an average of 14.65 faces per cell, the cells ranging from 9- to 21-hedra. Ninety-two combinations of cells were found; 85 occurred once, six occurred twice, one occurred three times. The types of faces ranged from triangles to decagons with a relatively low percentage of quadrilaterals, pentagons, and hexagons, and a relatively high percentage of other types.

2. The high number of faces was attributed to the occurrence of criss-crossed divisions, which are correlated with a wide distribution of face types. The cell plates of criss-crossed divisions have a high number of sides and this is also correlated with a high average number of faces.

3. An analysis of divisions by various types of cell plates was made, showing how these change the number of faces of cells in a mass. A cell plate with six sides will add 14 new faces to the cell mass for each division. Cell plates with fewer or more sides will lower or raise the number of faces added to the mass.

4. A study was made of pairs of faces in *Trillium* which lay in nearly the same plane. It was determined that these pairs consisted of faces of unequal area. Consideration of the two members of a pair as being one face, lowered the average number of faces to approximately 14 faces per cell. This was interpreted as being indicative of a tendency of the cells to maintain a stable arrangement.

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BOTANICAL BIBLIOGRAPHIES: CLASSIFICATION, FORM, ARRANGEMENT AND USE[1]

JACK MCCORMICK

A prerequisite for success in science is the ability to use the literature dealing with the research and concepts of ones contemporaries and predecessors. This literature, however, is virtually boundless and is continually gaining in bulk and diversity. The problem of locating information is particularly difficult in the biological sciences "which now contribute about half of the flow of new [scientific] publication" (Glass 1955). The library work of the biologist, however, is greatly facilitated by the bibliographic aids available to him. It is the object of this paper to describe the bibliographies available to the plant scientist.

To use a set of tools properly one must know the purpose for and limitations of each tool. So, too, with botanical bibliographies an appreciation of the basic types available is fundamental to their use. In developing the following classification, the general bibliographic analysis of Van Hoesen and Walter (1928) was extremely helpful.

Classification of botanical bibliographies with selected examples.[2]

1) Bibliographies of bibliographies of botany.[3] Besterman, Theodore. 1947. [Botanical bibliographies.] *In his* A world bibliography of bibliographies . . . , volume 1, columns 414–423. 2d ed., London, privately printed.

2) Comprehensive bibliographies with attempt to include every work published in the field of botany. Pritzel, Georg August. 1851. Thesaurus literature botanicae omnium gentium. Lipsiae. viii, 548 pp.

3) Comprehensive bibliographies of narrow scope, encompassing sharply delineated areas of botanical knowledge. Harvey, Rodney Beecher. 1936. An annotated bibliography of the low temperature relations of plants. Rev. Ed. Minneapolis, Burgess Publishing Co., ii, 240 pp.

4) Regional bibliographies which attempt to list all the botanical literature, or a specified portion of that literature, concerning a political or geographic area. Egler, Frank E. 1950. Regional vegetation literature. III. Massachusetts. Phytologia. 3: 193–237.

[1] The author wishes to thank Dr. Egbert H. Walker, Dr. Frank E. Egler, Dr. Murray F. Buell, and Mr. John Andresen for the helpful suggestions they made after reading the manuscript of this paper.

[2] The examples have been selected only with regard to their value as illustrations of the various types of bibliographies. Many fine botanical bibliographies are not mentioned.

[3] The writer is now compiling a bibliography of botanical bibliographies. He would like to contact anyone with contributions to the list.

5) Personal bibliographies containing lists of papers by or about a particular botanist. These lists are often appended to a biographical sketch or obituary. In these instances, the works are termed biobibliographies. Pool, Raymond J. 1915. A brief sketch of the life and work of Charles Edwin Bessey. Amer. Jour. Botany 2: 505–518.

6) Partial bibliographies of a botanical subject. These are often entitled "Contributions toward . . .," "A preliminary bibliography of . . .," or "Additions to . . ." They are designed to contribute to previously published bibliographies or to make available collected bibliographic information in a preliminary form. Bibliographies limited to a given period of years are also included in this type. [Gerard, W. R., and N. L. Britton.] 1880–1885. Contributions toward a list of the State and local floras of the United States. Bull. Torrey Bot. Club 7: 108–11; 8: 7–8, 16–19, 81–83; 9: 80–82; 10: 67–69, 103–105, 129–131; 11: 9, 43–44; 12: 26–28, 36, 98–100.

7) Selected bibliographies, designed to include only those works deemed by the compiler to be most useful to the audience for which the bibliography is intended. Bibliographies attached to text and reference works, designed to indicate the sources of more detailed information, are of this type. Lull, Howard W. 1953. Evapo-transpiration: excerpts from selected references. Vicksburg Infiltration Project. Southern Forest Experiment Station, Occasional Paper 131.

8) Bibliographies limited in scope and content to a definite phase within the field of botany, and further limited to works used and cited in the papers to which they are appended. These are usually titled, "Literature Cited."

9) Taxonomic indexes which give abbreviated (often cryptic) references to publications in which taxonomic entities have been described or pictured.

10) Journal indexes. Each journal index is limited to the material contained in certain volumes of a single periodical. The most useful indexes consist of either separate or integrated author, geographic, subject, and systematic indexes. References are usually in abbreviated style, giving only volume and page numbers. Their extremely limited scope and drastic abbreviation, coupled with the fact that one must consult the volumes indexed for publication date, full titles, covering pages, author's name, and other important data, allow their inclusion in a list of bibliographies only when the term "bibliography" is used in its broadest interpretation. Aikman, John M., and Frank C. Gates (Chairmen). 1952. Ecology Thirty Year Index (Volumes 1–30, 1920–1949). Pub. by Ecological Soc. of America. vi, 212 pp.

11) Special bibliographies covering such material as works still in manuscript, lists of government publications, library catalogs, etc. Atwood,

Alice C. 1908. Catalogue of the botanical library of John Donnell Smith presented in 1905 to the Smithsonian Institution. Contributions U. S. National Herbarium 12 (1): i–iii, 1–94.

The inclusion of abstracts or annotations adds to the usefulness without changing the classification of the bibliography. Annotations may be either critical, commenting on the value of the work or on its degree of completeness, or explanatory, supplementing the title to give a concise statement of the nature of the information contained in the reference, but not attempting to summarize that information. Abstracts, on the other hand, summarize all or the most pertinent portion of the information contained in the reference. The abstract may consist of phrases quoted from the text of the reference or of an original summary written by the bibliographer.

Within any bibliography, regardless of the class into which it falls, there are four main choices for the primary internal arrangement (McCrum and Jones 1954): 1) Chronological arrangement by date of publication. 2) Alphabetical arrangement, a) By author's name, b) By title, c) By subject (especially in indexes), d) By place of publication (journal name). 3) Geographical arrangement by political division or natural region with which the literature is concerned. 4) Topical arrangement, classifying references into several subject-matter categories.

Following the primary division there may be a secondary and a tertiary division of the references, allowing a hierarchical arrangement. Further arrangements are possible if the bibliography is indexed. For example, in the series of bibliographies of regional vegetation literature to be published by The American Museum of Natural History a geographic arrangement has been chosen as primary; a chronologic arrangement will be used for references pertaining to a geographic subregion; and when more than one title is listed for a given year, the references will be listed alphabetically by the authors' names. An author index, employing an alphabetical arrangement, will accompany each bibliography.

A few bibliographies combine author, subject and geographical arrangements in equal rank, listing the entires alphabetically. This is a practice used principally in large catalogs which would otherwise require an unwieldy index.

Occasionally consecutive numbers are assigned to the entries in a bibliography, irrespective of its arrangement. The numbers are employed for brevity in indexing. An index which employs such a numbering system, however, is a burden to the user in that the numbers convey no idea of the identity of the references, necessitating an individual inspection of each entry to determine its usefulness. In addition, any typographical errors which occur in such an index constitute virtually unsolvable enigmas and

result in "lost" references. Similar criticisms can be made of journals which require the use of numbers to refer to literature cited in the text.

Physically, bibliographies assume one of five forms:

1) *Card files.* Many investigators, and perhaps all libraries, enter their references or accessions on small cards or paper slips. Catalogs of this type are easily rearranged; additions are easily made; storage units are neat, compact, and easily obtainable; and in manuscript bibliographies the cost of individual entries is kept at a minimum.

The few published bibliographies that are, or have been, issued on cards are too expensive for the individual to purchase.

Within recent years a few investigators have begun using punched cards. These cards allow a complex system of cross-referencing without increasing the number of cards used. There are several disadvantages associated with punched cards which, in the opinion of the writer, outweigh their advantages for an individual's files.

2) *Loose-leaf catalogs.* A few investigators, especially those who make long abstracts, enter references upon large loose-leaf pages. The sheets are kept in regular loose-leaf binders. If the individual references are entered on separate sheets, this system has the same flexibility of arrangement as the card file. Loose-leaf references, however, are more expensive and are much less easily stored than carded references.

3) *Journal papers.* Shorter bibliographies and certain specialized bibliographies may be published in periodicals. The publication of a bibliography in an appropriate journal makes it immediately available, without extra cost, to the investigators who should find it of most value. Author's reprints allow distribution of copies of the bibliography to an additional number of workers known to, or in correspondence with, the author.

4) *Periodical bibliographic publications.* Several bibliographies of current literature are issued at regular intervals and are sold on a subscription basis, primarily to libraries. These bibliographies may be indexed in each issue or annually or semi-annually at the end of a volume. Periodical bibliographies are for the most part very broad in their coverage, and are extremely voluminous. Since each issue or volume is usually indexed separately, one must consult each issue or volume separately for references.

5) *Pamphlets, books, and processed publications.* Lengthy bibliographies or bibliographies of sufficient interest to, or undertaken at the request of membership organizations, institutions, foundations, or commercial concerns may be issued in book or pamphlet form. These books are relatively expensive, little advertised, usually printed in limited editions, and rarely reprinted. The compiler may publish his own bibliography in book form; but more often than not, he will mimeograph or otherwise duplicate the

bibliography for limited distribution to classes, at meetings, etc. Processed bibliographies are rarely listed in the standard indexes and are too often not distributed to libraries.

The use of bibliographic tools will be facilitated by an understanding of the several types of bibliographies available and the variations of arrangement possible within them. Furthermore, an understanding of the basic principles of botanical bibliography should profit individuals who plan to compile bibliographies. A greater awareness of the variety possible in bibliographic format and arrangement should permit a more logical determination of the style best suited to a particular need.

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TORREYA

A Large Swamp White Oak of the Lower Raritan Flood Plain[1]

JOHN W. ANDRESEN

Swamp white oak (*Quercus bicolor* Willd.) a large infrequent member of the Leucobalanus complex has been reported as having attained diameters of considerable proportions. Sargent (1933) lists the diameter of the largest swamp white oak at between 8 and 9 feet, Harlow and Harrar (1950) note a maximum diameter of 7 feet, and Illick (1928) states the largest diameter of this species in Pennsylvania at breast height (d.b.h.) is 5.2 feet. These representative measurements are perhaps a bit more accurate than the myriads of popularized book descriptions of trees often times based on hearsay without investigating the precise size and location of the particular tree they report to be the largest member of a species. In the present paper, the author describes what he believes to be the largest swamp white oak in New Jersey and one of the largest living specimens if not the largest of this species in the northeastern United States.

The purpose of this paper is to identify and record the present tree before it is destroyed. In this discussion, the Johnson Park *Q. bicolor* will be referred to as the large oak.

The gross shape and size of the large oak is shown in Fig. 1. Its vital statistics are: diameter, 59.9 inches 4½ feet above the current fill surface, total height, 72 feet; and average crown spread, 71 feet. Its geographic coordinates are 74°26′52″ W. long. and 40°31′20″ N. lat. More specifically the large oak is located 790 feet S 30°E from the park headquarters building. The property upon which the tree stands which is largely in Piscataway Township, Middlesex County, is known at present as Johnson Park. Prior to the Johnson Foundation donation in 1936, the area consisted of a poorly drained river swamp spotted with grass and sedge meadows. Subsequent to acquisition, the Middlesex County Park Commission began to have the depressions filled, in some places as deep as 5 feet, with broken tile, cinders and gravel. The soil immediately surrounding the large oak is azonal and known as Rowland silt loam (Quakenbush 1955). On top of the soil is a 1-foot layer of broken tile upon which a yearly inch of coarse gravel is added by the Park Department. Even with this ever-increasing elevation of land suface, several times a year the park is subject to inundation by 2 or 3 feet of water.

From the form of the large oak, apparently one at least and probably two or three clear cuttings of the larger trees in the swamp have been made. Three huge low-hanging branches 2 to 3 feet in diameter were cut about 15 years ago to assure pedestrian safety. They attest to the early open growth habit of the tree assumed to be now between 240 and 300 years old. The computed age of the tree was based on the formula of 8 to 10 annual rings (observed by an increment boring) per transverse inch times 30 inches, or the product of the radius and the aveage rate of growth. If this assumption is correct, the limby form of the tree would suggest there was intensive cutting of the swamp forests in the region for timber and fuel during the late 1600's and early 1700's. It may also be conjectured from local history that the cuttings took place circa 1700, 1800, and 1890–1900 (Table 1.). The circumjacent trees (Table 1a.) are tall, straight, and limbless for ½ to ⅔ of their total heights and present the appearance of being forest grown (Fig. 1.) The age grouping of between 50 and 63 years of the adjoining trees (with none older except for a few considered of poor form for timber) also supports the contention of a virtual clear cutting about the turn of the 20th century. A study (Table 1b.) of 7 stumps of American

[1] Paper of the Journal Series, New Jersey Agricultural Experiment Station, Rutgers University, the State University of New Jersey, Department of Forestry, New Brunswick.

elm that had been cut because of death by Dutch Elm disease revealed 1 tree in the 30-year class, 3 in the 50-year class, and 3 in the 80-year class. Since these trees were near a main road and about 200 yards from the large oak, the cuttings which released them may have taken place at other times than those near the large oak, although the 50-year class ties in with the presumed cutting of 1890–1900. Since there is now a total lack of reproduction, the only way to restock the park is by planting. Although the absence of saplings suggests rather severe grazing, this postulation may be discounted in view of clearing and bulldozing operations when the park was graded.

Table 1. *Age and d.b.h. of (a) species of trees found in immediate area of large oak; and (b) data of cut Ulmus americana 300 yards north of large oak.*

(a.) Species	Age	d.b.h.	(b.) Age	d.b.h.
Fraxinus americana	64	14.0	86	21.0
Quercus palastris	63	13.0	85	16.0
Juglans nigra	63	15.1	81	24.1
Ulmus americana	60	12.2	57	22.3
U. americana	57	13.0	56	18.0
Gleditsia triacanthos	57	18.6	56	10.1
Tilia americana	50	13.0	31	6.5

Other members of the natural forest community in decreasing order of presence in the vicinity of the large swamp white oak are: pin oak (*Q. palustis*) which is numerically equal to the total of all of the following trees, American elm (*Ulmus americana*), white ash (*Fraxinus americana*), honey locust (*Gleditsia triacanthos*), white oak (*Quercus alba*), American basswood (*Tilia americana*), red maple (*Acer rubrum*), black willow (*Salix nigra*), and black walnut (*Juglans nigra*). Buell and Wistendahl (1955) in their study of the forests of the upper Raritan flood plain, list these same species, but their list is much richer in number of species. Perhaps the additional species in their list are not found in Johnson Park because of frequent and recent clearing and cutting there. Although Buell and Wistendahl did find an occasional swamp white oak, they gave no ages of the trees. Wistendahl (1955), however, in studying old-field succession along the Raritan determined ages for white ash up to 35 years but gave the ages of no other large trees. He also found that swamp white oak was unimportant in the species composition of the Raritan flood plain.

An increment boring of the large oak revealed 48 years of growth for the outer 4¾ inches of xylem with 18 years in the outermost inch. Yearly growth has decelerated rapidly in the last ten years and is perhaps due to a combination of the continued filling about the tree, the compaction of the "soil" by the thousands of park visitors, plus children's "Indian" fires at the tree's base, and a natural decadence of the tree which is also indicated by a fecundal deterioration (no acorns at all for the last 2 years). The bit of the borer sank into decayed wood after five inches of penetration. From this fact and the evidence of basal rot and decay in the large branch scars, it is inferred that the tree is now quite hollow.

The once majestic flood plain forests of the Raritan River are but memories and before all the vegetation is destroyed by man's "cultural" operations, studies similar to Buell and Wistendahl's (1955) and Wistendahl's should be made of the remaining forests. The residual forests are not only valuable from floristic and vegetational aspects, but also harbor an extremely diverse avian population. The birds may well be driven away when and if contemplated plans are carried out for creating a public park of the flood plains from Highland Park to Bound Brook (a strip 6 miles long and in places about 300 yards wide). Some of the largest river birch (*Betula nigra*) and sycamore (*Platanus occidentalis*) in New Jersey are to be found on this proposed park site. A unique thicket of black alder (*Alnus glutinosa*) which grows near another large swamp

white oak lies in the construction path of a trunk sewer that will reach the trees during the coming year.

It is sincerely hoped that some of these invaluable vegetational areas will be left as natural areas, but the pressures of increasing population, proposed industrial expansion and road building, sewer construction, and other "progressive refinements" seem to preclude the saving of any natural areas from Somerville to Raritan Bay. Perhaps State legislation is the one sure way to preserve trees like the large oak and the rapidly vanishing natural vegetation. Such laws should perpetually assure and provide for the protection and maintenance of such natural phenomena.

FIG. 1. The large *Q. bicolor* showing its open grown habit. Other members of the stand are tall, straight and devoid of limbs on the lower half. The range pole is calibrated in one foot intervals.

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Field Trip Reports

March 25. St. John's in the Wilderness. A joint Torrey-Rockland Audubon group attended this service (see Torreya in Bull. Torrey Club 81: 460, 1954, and 82: 397, 1955). An unseasonably late blizzard had left over a foot of snow which made the day more conducive to skiing than to botanizing in the usual sense. However, a pre-service walk on the snow covered trails afforded an excellent opportunity to observe the winter condition of woody plants and particularly their response to the prevailing ecological condition. Attendance: Torrey 4, Rockland Audubon 10. Leader, J. Harry Lehr.

April 7. Long Branch to Toms River, N. J. This trip was also one for the ecologists, with a storm running that set up breakers on Wreck Pond. Breakers rolled completely over the red metal buoy at the end of Manasquan jetty and down each of the metal barriers protecting the shore. No "early wildflowers" were reported but 21 waterfowl were observed, including snow goose, whistling swan, and Holboell's grebe. Mr. Wisner joined the group at Long Branch and took us to Lake Tachanassee and then to his home where elaborate bird feeding facilities are operated. The bird list then mounted, the better ones being downy woodpecker, phoebe, chickadee, titmouse, evening grossbeak, purple finch, towhee, dickcissel, and great horned owl. Total bird list, 44 species. Attendance 9. Leader, Barbara Cook.

April 22. Lehr's Residence, Tallman, N. Y. A Rockland Audubon trip through this area on April 24, 1955 produced a list of 26 early spring flowering species. This year, see weather reported above, only six species were found in bloom. Fortunately for those who had not seen the plant before, a single specimen of *Trollius laxus* (globe flower) was found in bloom. Attendance: Torrey 10, Rockland Audubon 4. Leader, J. Harry Lehr.

May 5. Raritan, N. J. This portion of the Raritan river flood plain was seen under ideal conditions for the spring season. Mertensia was at height of flowering and the stand was as dense and luxuriant as ever. There was no wind throw damage from the hurricanes of last August but the height of the flooded Raritan was evident from debris in the branches of the trees. Attendance 5. Leader, J. A. Small.

May 6. Inwood Park, N. Y. On previous trips it has been possible to find Dutchman's breeches in this park but none was located this year. The group did discover Kenilworth ivy growing on an abandoned foundation and it was in bloom. A good bird list was developed with the blue-grey gnatcatcher the species of greatest interest. Attendance 6. Leader, Jane Meyer.

May 13. William T. Davis Wildlife Refuge, Staten Island, N. Y. We studied the usual woodland and field areas. There were many spring flowers in evidence such as trout lily, jack-in-the-pulpit, shadbush, spring beauty, etc. The 2 plants of *Clematis ochreleuca* which had been transplanted into the refuge last year were doing well. The nest of a mallard duck was discovered on a meadow near New Springville creek. There were 9 eggs. Attendance 14. Leader, Mathilde Weingartner.

May 26. Great Kills Marine Park, Staten Island, N. Y. *Hudsonia tomentosa* was found but not not yet in bloom. However a number of flowering plants of *Krigia virginica* were found on the dry sandy soil. Many migrating shore birds were seen, among them

least tern, common tern, knot, and dowitcher. Attendance 10. Leader, Mathilde Weingartner.

May 27. Appalachian Trail north of Blairstown. The weather was too inclement for trail clearing and painting activity but an interesting walk was enjoyed. Highway construction had Millbrook road in a bad state on the mountain top. At the Flatbrookville road intersection with the Appalachian Trail there is an active real estate development. It has not seriously interfered with the Trail yet. Spring flowers of the season along the Trail were found. Some frost damage to recently emerged foilage was noticed on some species, even oaks and hickory. The hurricanes of last August had done little damage. Attendance 1. Leader, John A. Small.

PROCEEDINGS OF THE CLUB

March 20. The meeting of the Club, at Columbia University, was called to order by President Barton at 8:05 P.M. Sixteen persons were present. The minutes of the previous meeting were read and approved.

President Barton introduced the speaker of the evening, Dr. Bassett Maguire of the New York Botanical Gardens, who addressed the Club on a "Report on Some Compositae on Guayana Highland with Reference to their Geographic Distribution." The talk was of great interest to the members as evidenced by the active discussion period which followed the talk.

The meeting was adjourned at 9:15 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

April 12. The meeting was called to order at 8 P.M. at Fordham University by President Barton. Sixty-five members and guests attended. The minutes of the meeting of March 20 were approved as read.

Mr. William P. Martin, Dr. Knut J. Norstag, and Mr. Edward J. Wheeler were elected to active membership; Mrs. Louis Levine was elected to associate membership. The resignation of Dr. G. Steiner was announced.

The scientific program consisted of a stimulating talk by Dr. P. Maheshwari, Professor of Botany and Dean of the Faculty of Science at the University of Delhi, India on "Pollen, Pollen Tube, and Embryo." Discussion of Dr. Maheshwari's presentation continued until 10:15, over refreshments generously provided by the Biology Department of Fordham University.

Respectfully submitted
Edwin B. Matzke
Secetary Pro Tem

May 1. The meeting was called to order by President Barton at Columbia University at 8 P.M. Forty members and guests were present. The minutes of the meeting of April 12 were approved as read.

Since there was no business to be conducted, Dr. Barton introduced the speaker of the evening, Dr. Joseph Copeland of the City College of New York who spoke to the club on "Insectivorous Plants." The talk was well illustrated and brought forth many questions in the discussion period which followed.

The meeting was adjourned at 9:05 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

BOOK REVIEWS

Medical Research: A Midcentury Survey. American Medical Research: in principle and practice. The American Foundation. 1,504 pp. 2 volumes.

J. and A. Churchill Ltd., London; Little, Brown and Company, Boston and Toronto, 1955. $15.00.

This compilation of data on basic research has been assembled by a staff of editors and more than 25 experts in various phases of medical research. The report brings together the pertinent data on basic reseach, but workers in the field of medicine are not the only ones for whom the two volumes were written. Biologists will be interested in them, as will thousands of laymen.

The chapters of the first volume discuss: 1) Medical research in the perspective of biological, chemical, physical, and mathematical science; 2) Current trends in medical research in the United States; 3) Research agencies; 4) Publication of the results of research. The first chapter is largely devoted to contributions of atomic energy research in biology and medicine, discussing the cooperation of universities with the Atomic Energy Commission, as well as applications in agriculture, use of isotopes in the study and treatment of certain diseases and genetic effects of radiation.

In the second chapter pertinent data are presented on agencies that support basic research: foundations, pharmaceutical laboratories, independently endowed institutes and universities. Among problems presented in this chapter are the advantages and disadvantages of planned (coordinated) basic research; work on projects and team research; governmental support of medical research; the creation and functioning of the National Science Foundation and of its fellowship program; security regulations, procedures in classified work and the effect of these on research and researchers.

The third chapter, on universities and medical schools, presents in its first 100 pages contributions to medicine from research in biology and in other fields. An additional 200 pages of this chapter present research at medical schools of privately endowed universities (Chicago, Columbia, Johns Hopkins, Harvard, Pennsylvania, Rochester, Washington University, Yale, New York University, Cornell), and at tax-supported medical schools in Wisconsin, California, Illinois and Michigan. Other schools are briefly mentioned.

The discussion of botany in this chapter will be of particular interest to those working in the plant sciences. Contributions of botany to the solution of medical problems are illustrated through investigations at the molecular and cellular levels. Although none of the 73 schools of medicine in the U. S. A. maintain botany departments or botany research laboratories, botanists have nevertheless contributed toward an understanding of clinical problems and basic processes. Several spectacular discoveries of recent years in the field of antibiotics were made by botanists. Penicillin, streptomycin, aureomycin and terramycin produced by fungi represent only a few of the most recent discoveries in a long succession of biological and medical contributions related to botany. The foundations of current concepts of immunity and resistance, the basis of contemporary research in metabolism, the uses of Neurospora and yeasts in biochemical genetics are other examples of botanical research related to medicine.

The important role played by foundations in American medical research, the policies of various foundations, methods of spending money in capital grants, fluid funds, fellowships and term grants, are presented in great detail. The final pages of the third chapter deal with independent research institutes, industrial organizations, government, and scientific and professional societies.

The comparatively short fourth chapter on "clearing results and controlling products of medical research" has interesting data on literature reviews, conferences and symposia, abstracting, microfilming and international exchange of literature and of scientists.

The chapters of the second volume discuss several unsolved clinical problems. The first chapter deals with current metabolic concepts, nucleic acids, enzymes, proteins, and hormones.

Cancer and factors that influence normal and abnormal growth are discussed in the second chapter. The etiology of cancer is still obscure but four promising experimental approaches to the problem are skillfully presented. They deal with chemical carcinogens, hormones, enzymes, and viruses. The chapter ends with a stimulating presentation of

theories influencing cancer research and of the pertinence of the various concepts on human cancer.

Infertility and its various causes are presented in the third chapter. Arteriosclerosis and its association with cardiovascular deaths, the work on cholesterol and its metabolism, as well as current research on structure and function of arterial tissues are presented in the fourth chapter.

Hypertension is the subject of the fifth chapter. Although recent years have brought dramatic developments in new blood-pressure-reducing drugs, obtaind from various plants, the mechanism of action of these potent substances remains unknown.

Rheumatic syndromes are the subject of chapter 6. Tuberculosis and its control by vaccination, drugs, nutrition and surgery are the topics of chapter 7.

Viruses and virus diseases and the interaction of the invading agent and the invaded host are treated in chapter 8. Some of the more than 70 subtitles of this long chapter will illustrate the wide range of subjects covered: Scope of the virus problem in biology and medicine; hypothetical viruses; viruses studied rather as research tools than as agents of disease—vaccinia, bacteriophage; virus workers and centers of virus work; money spent for virus research; the nature of viruses; attempts at classification; characteristics of viruses and their behavior in the cell; purification of viruses; virus strains and variations; virus interrelations; methods of virus transmission; susceptibility and resistance to virus infections; chemotherapy and chemoprophylaxis in virus diseases.

The virus chapter clearly presents the wide interaction of various fields of research. The discussion will be valuable both to workers in the field and to those seeking first-hand information concerning it. There are good reasons for the manifold interest in viruses: Bacteriologists are involved because certain viruses destroy bacteria; pathologists are interested because viruses cause diseases; chemists because of the properties of macromolecules and the suitability of chemical methods in virus purification; geneticists because viruses in some respects appear to parallel genes and because they can mutate and hybridize, and more recently because of their abilities in changing the heredity of bacteria by transduction; philosophers even are concerned with viruses because here they hope to find an answer to the perennial question: What is life?

The last two chapters of the second volume cover the subjects of alcoholism and schizophrenia.

The two volumes bring out clearly the fact that all fields of biology are important to medicine. If it were not for Mendel's studies on peas we should know little of the principles of sex determination and heredity in man. Discoveries in the field of permeabilty of cell membranes in algae, the independent life of cells in tissue culture and many other fundamental discoveries had repercussions throughout the entire realm of the biological sciences and especially in medicine.

A few shortcomings were noticed where the work of investigators had been taken from standard textbooks and review articles; the reader is seldom referred to the original literature that might help him obtain direct information or background. The sources, listed for each chapter at the end of the volumes, are not always up-to-date. Thus, for instance, information on research institutes lists as most recent information on the Carnegie Institution of Washington the Yearbook 1950, for the biological Laboratory at Cold Spring Harbor an article in 1944, and for the Rockefeller Institute for Medical Research Descriptive Pamphlets 1944 to 1951. Although considerable care was given to the printing of the book and a fairly complete table of contents was included, no adequate index was provided. The authors of the chapters are not identified. Despite these few shortcomings, the editor, Esther Everett Lape, and all the authors are to be congratulated upon the preparation of such an extensive compendium on the relationship of basic research in all fields to medical progress.—KARL MARAMOROSCH, The Rockefeller Institute for Medical Research, New York, New York.

Guide to the Flora of Malta. By Guido G. Lanfranco. 66 pages plus 300 figs. on 33 plates. Progress Press Co., Ltd. Malta. 1955. 6 s/ 6d.

This paper bound treatise is said to be for the beginner studying Maltese flora. It

would be unfortunate to claim anything more for it. The 300 (296 flowering plants) species to which it is limited are grouped by color, thereby turning up some strange taxonomic bedfellows on the same plate. Thirty-nine pages of more or less captions for the later plates are followed by an index of Latin names, an index of English vernacular names, an index of Maltese vernacular names, and a classification (taxonomic) of the species included. Species are consistently numbered so that reference may be made from the lists to the figures (line drawings) which are the only means of identification.

Around 1000 flowering species are known from Malta and a slightly larger number of Cryptogams. A more complete work is that of Prof. John Borg, "Descriptive Flora of the Maltese Islands," published in 1927.—J. A. S.

Ferns of Tennessee: with the Fern Allies Excluded. By Jesse M. Shaver. xviii plus 502 pages. George Peabody College for Teachers, Nashville. 1954. $6.00.

It is gratifying to have another state fern flora available and this one appears particularly well done. Originally intended to include "fern allies", these had to be omitted, unfortunately, due to the author's injury. It may be of interest to others that this publication was effected by first publishing the material serially in the Journal of the Tennessee Academy of Sciences. Reprints were obtained with changed pagination, etc., so as to be bound later into the present work. With some grants in aid it was thus possible to treat the 63 species recognized over a period of 13 years, 1942–1954. The size of the book attests to the completenss of the treatment. It's perusal will convince one of the author's thoroughness in searching for and in studying the fern flora of the state. There are nearly 250 figures, including half-tone habit photos, line drawings, and distribution maps.

To illustrate with a well-known example, the New York fern, *Thelypteris noveboracensis* (L.) Nieuwl., a short general description is followed by a detailed description of nearly two pages. There is also a full-page half-tone habit view, a full-page figure with five drawings, a distribution map showing that the species has been found in nearly every county, and a bibliography of 17 titles. The distribution outside of Tennessee is given in general terms.

There is a discussion of the variants of certain species and notes such as the reportedly extensive rootstock system of *Pteridium* make it clear that Shaver really dug around. At the back of the book 34 pages are required to list the known distribution of the fern species in Tennessee. A glossary is then followed by an index to latin names and another to the common names.—J. A. S.

The Genus Achlya: Morphology and Taxonomy. By Terry W. Johnson, Jr. xvi plus 180 pages, including 22 plates. The University of Michigan Press. 1956. $4.50.

A critical review evaluating this monograph will not be attempted here. I am not competent and such a review would be only one man's opinion. Men's opinions differ markedly in the delimitation of species. Monographing and reassessing the taxonomy of fungi is always a task of recognized difficulty due to unsatisfactory, if any, reference material upon which earlier descriptions have been based. In this monograph, the usual, rapid historical resume is followed by a statement about collecting and culturing these water molds that will prove valuable to anyone wishing to grow them, and they do make interesting class material.

Three subgenera are recognized: Achlya, Centroachlya, and Subcentrica. A total of 35 species (one with two varieties) are found in the keys. Each species is treated as to origin (original publication), synonomy, morphology, material examined (living), recorded collections, and miscellaneous comments. There is also a section dealing with taxa of doubtful affinities, where 10 taxa are discussed and this is followed by 17 excluded

taxa. A 13-page bibliography precedes the plates which appear to be carefully drawn and faithfully reproduced. There is an index.—J. A. S.

A Laboratory Manual for General Botany. By E. W. Sinnott and K. S. Wilson. xvi plus 333 pages. McGraw-Hill. 1956. $3.00.

Although designed for use with their "Botany: Principles and Problems" (1955), the authors believe this manual to be sufficiently flexible in scope to be used with success where other textbooks are adopted. Reference is made to no other source material however. Even "Botany" is referred to only by chapter when approaching the appropriate sequence of excercises. There are a total of 103 exercises. Most of them are common to other manuals of this subject but a few interesting novelties are to be found. Drawings are called for frequently; very few are provided. There are many questions to be answered, always a feature of Sinnott's approach. The book is bound, with paper cover, but perforated to tear out as 8 × 11 inch pages punched for a three-ring binder.—J. A. S.

Plant Ecology Workbook. By J. T. Curtis. iv plus 87 pages. Burgess Publishing Co. 1956. $3.25.

There are fewer manuals for laboratory and field work in plant ecology than in general botany. No doubt there are fewer such courses offered but also there is undoubtedly much more individuality to such courses. As field courses they must reflect the locality where given as well as the special interests of the instructor. The present manual offers 12 exercises. It was surprising to find 9 of them designed for laboratory or greenhouse use, sometimes employing mapped populations. Designed particularly for a large state university in the north central states, it may be that field work is largely unseasonal to the course and it may be difficult to administer with large classes. Each exercise has an introduction, detailed directions for procedure, the call for a report, and a few references. Data sheets are generously provided and the compilation of class data for further analysis is encouraged. A statement of equipment and supplies needed will prove useful to both instructor and student.

Following the exercises, there is a 30-page section of reference materials consisting of field keys (to stump woods, trees in winter, shrubs in winter, trees in summer, shrubs in summer, and grasses), maps, and conversion tables (relative humidity from psychrometer readings, vapor pressure deficit from humidity, circumference to basal area, and diameter to basal area). The final section is 9 pages of literature references. A back cover pocket contains distribution maps of species in representative northern hardwood forest, maple forest, and tall grass prairie. The pages are processed, and numbered, on one side only thus providing abundant space for addenda and annotations. The book is spiral bound, with flexible cover.

Upon completing the perusal of this manual I was perplexed. It is sound, factual. But it is orthodox to a point beyond merely conservative where I was looking for a dynamic and progressive approach reflecting that of the department and the staff from which it originated. The author is internationally known for his field work and for his progressive ideas about vegetation but this course can apparently be completed with practically no experience in the field.—JOHN A. SMALL, Douglass College, Rutgers, The State University of New Jersey.

NOTE

Another Index

Ecological Monographs: Twenty-year Index covering volumes 1–20 (1931–1950) is now added to the long term indices (See Torreya for last May). This latest one is a committee job headed by Donald B. and Elizabeth G. Lawerence. In addition to authors and important words from the titles, the work lists names of organisms, methods, maps and other illustrative materials, instruments, and geographical locations. It is available paper bound from Duke University Press for $2.50.

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INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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